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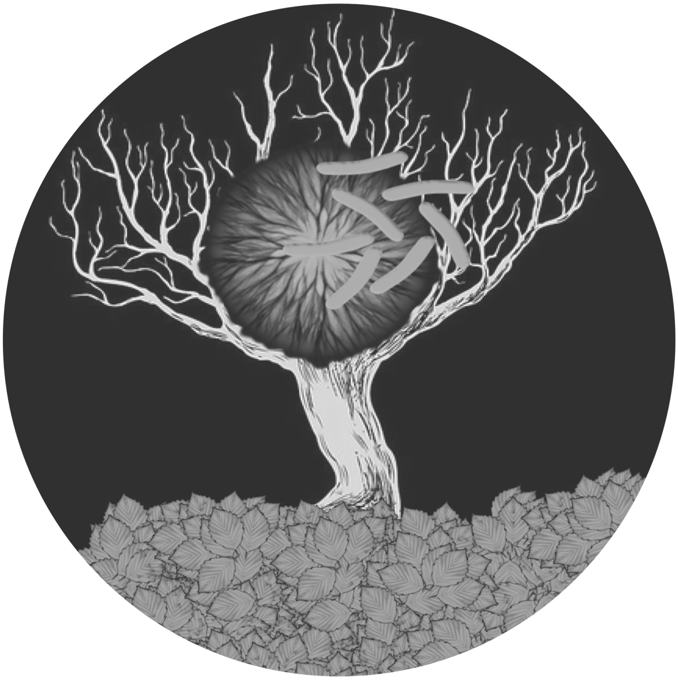
# From forests to microbiomes

## The mediation of plant-soil systems by root-symbiotic fungi

TARQUIN NETHERWAY



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## The mediation of plant-soil systems by root-symbiotic fungi

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# From forests to microbiomes. The mediation of plant-soil systems by root-symbiotic fungi

## Abstract

Plant-microbial symbioses play crucial roles in ecological and biogeochemical processes such as carbon and nutrient cycling, plant-soil feedback, and evolutionary dynamics. However, less is known about how these symbioses influence the broader soil microbial communities (microbiomes) that they interact with, which is essential to understanding the ecosystem processes they facilitate.

In this thesis, I investigate the effect of mycorrhizal type and other root symbioses on the structure and potential function of belowground microbiomes, as well as leaf microbiomes and leaf element concentrations. To accomplish this, I used a variety of techniques, including metabarcoding and metagenomic analysis of microbial communities and their functional genes from field studies at various scales, from single vegetation communities to a European latitudinal gradient.

Regionally, I found that sites dominated by arbuscular mycorrhizal (AM) vegetation had relatively more AM fungi, bacteria, fungal saprotrophs, and pathogens in their soils compared to ectomycorrhizal (EcM) vegetation, and that coniferous EcM vegetation was a particularly important determinant of soil conditions and microbiome features. I also found that root colonization by dark septate endophytic (DSE) fungi was strongly associated with the composition of microbial communities and functional genes, including a negative relationship with the relative abundance of fungal pathogens and bacteria across Europe. Lastly, I found that tree species with different root symbioses and levels of colonization and their leaf element profiles were a key factor shaping leaf microbial communities and diversity compared to climate, with contrasting relative abundances of bacterial and fungal guilds and taxa between and within tree species.

Overall, my findings suggest that the biotic interactions between plants and their root symbionts are important factors determining the structure and function of microbiomes across vegetation communities and tree species, with implications for wider ecosystem processes.

Keywords: plant-soil systems, root symbiosis, ectomycorrhiza, arbuscular mycorrhiza, nutrient-acquisition strategies, fungi, bacteria, soil microbiome, leaf microbiome, metagenomics

# Från skogar till mikrobiom. Hur växt-marksystem samspelar med rot-symbiotiska svampar

## Sammanfattning

Symbioser mellan växter och mikrober spelar en avgörande roll för ekologiska och biogeokemiska processer som kol- och näringsämnenas kretslopp, växt-mark-interaktioner och evolutionär dynamik. Det är emellertid mindre känt hur dessa symbioser påverkar de mikrobsamhällen—mikrobiom—som de interagerar med i marken, vilket är viktigt för att förstå hur de påverkar olika ekosystemprocesser.

I denna avhandling undersöker jag effekten av växters, främst träds, olika typer av symbioser med mykorrhizasvampar och andra rotsymbioser på sammansättning, struktur och den potentiella funktionen hos mark- och bladmikrobiomer samt bladens stökiometri och innehåll av olika näringsämnen. Jag har gjort fältstudier på olika skalor, från bestånd i olika habitat till en geografisk N-S gradient över hela Europa, och använt olika molekylärbiologiska tekniker, såsom metabarcoding och metagenomisk analys av mikrobsamhällen och deras funktionella gener.

Resultaten visar att på platser med vegetationstyper som dominerades av växter med arbuskulär mykorrhizasymbios (AM) fanns det relativt fler AM-svampar, bakterier, svamp-saprotrofer (nedbrytare) samt växtpatogener i marken jämfört med vegetationstyper som dominerades av växter med ektomykorrhizasymbioser (EcM), såsom barrskogsdominerade habitat. Jag fann också att rotkolonisering av mörka septatsvampar (DSE) över hela Europa var starkt associerad med mikrobsamhällenas sammansättning och funktionella gener, inklusive ett negativt samband med den relativa abundansen av svamppatogener och bakterier. Slutligen fann jag att trädarter och deras innehåll av olika näringsämnen till större del än klimatvariabler kunde förklara mikrobsamhällens sammansättning och mångfald på bladen.

Sammantaget antyder mina resultat att interaktioner mellan växter och deras rotsymbionter är en viktig faktor som påverkar strukturen och funktionen hos mikrobiomer över hela vegetationssamhällen såväl som hos enskilda träd, vilket kan ha implikationer för många ekosystemprocesser.

Keywords: (växt-jordsystem, rotsymbios, ektomykorrhiza, arbuskulär mykorrhiza, mörk-septat endofyter, näringsstrategier, svampar, bakterier, mikrobiom, metagenomik)

# Dedication

To my late father who instilled within me the curiosity to find out what lies below the surface via the nether way.

*Sheriff, what kind of fantastic trees have you got growing around here? Big, majestic.*
- FBI Special Agent Dale Cooper

# Contents

# List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Netherway, T., Bengtsson, J., Krab, E. J., & Bahram, M. (2021). Biotic interactions with mycorrhizal systems as extended nutrient acquisition strategies shaping forest soil communities and functions. *Basic and Applied Ecology*, *50*, 25-42.

II. Bahram, M., Netherway, T., Hildebrand, F., Pritsch, K., Drenkhan, R., Loit, K., Anslan, S., Bork, P. & Tedersoo, L. (2020). Plant nutrient-acquisition strategies drive topsoil microbiome structure and function. *New Phytologist*, *227*(4), 1189-1199.

III. Netherway, T., Bengtsson, J., Buegger, F., Fritscher, J., Oja, J., Pritsch, K., Hildebrand, F., Krab, E. J., & Bahram, M. Root-associated fungi shape tree root and soil microbiomes across a latitudinal gradient in Europe. (submitted)

IV. Netherway, T., Krab, E. J., & Bahram, M. Leaf element profiles and microbiomes of trees with differing root symbioses across Europe. (manuscript)

Paper I is open access under the Creative Commons Attribution 4.0 International Licence (CC BY-NC-ND 4.0), and Paper II is reproduced with the permission of the publisher.

The contribution of Tarquin Netherway to the papers included in this thesis was as follows:

I. Led the development of the ideas, performed the literature review, created the figures, and led the writing of the manuscript.

II. Participated in the analysis of the data and writing of the manuscript.

III. Led the development of the ideas and design of the study, performed the field work, performed the microscopic analysis of ectomycorrhizal colonization, performed the molecular lab work on soil samples, led the data analysis, created the figures, and led the writing of the manuscript.

IV. Led the development of the ideas and design of the study, performed the field work, analyzed the data, created the figures, and led the writing of the manuscript.

During this doctorate, Tarquin Netherway contributed to the following papers and book chapter not included in the thesis:

I. Põlme *et al*. (2020). FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity*, *105*, 1-16.

II. Bahram, M., Netherway, T., Frioux, C., Ferretti, P., Coelho, L. P., Geisen, S., Bork. P., & Hildebrand, F. (2021). Metagenomic assessment of the global diversity and distribution of bacteria and fungi. *Environmental Microbiology*, *23*(1), 316-326.

III. Sveen, T. R., Netherway, T., Juhanson, J., Oja, J., Borgström, P., Viketoft, M., Strengbom, J., Bommarco, R., Clemmensen, K., Hallin, S., & Bahram, M. (2021). Plant-microbe interactions in response to grassland herbivory and nitrogen eutrophication. *Soil Biology and Biochemistry*, *156*, 108208

IV. Netherway, T., & Bahram, M. (2021). Fungal Biogeography. In *Biogeography: an integrative approach of the evolution of living* (pp. 193-218). New Jersey: Wiley.

V. Tedersoo *et al*. (2021). The Global Soil Mycobiome consortium dataset for boosting fungal diversity research. *Fungal Diversity*, *111*, 573-588.

VI. Tedersoo *et al*. (2022). Global patterns in endemicity and vulnerability of soil fungi. *Global Change Biology*, *28*(22), 6696-6710.

VII. Bahram, M., & Netherway, T. (2022). Fungi as mediators linking organisms and ecosystems. *FEMS Microbiology Reviews*, *46*(2), fuab058.

# Abbreviations

| | |
|---|---|
| AM | Arbuscular mycorrhiza |
| EcM | Ectomycorrhiza |
| C | Carbon |
| Ca | Calcium |
| CAZyme | Carbohydrate active enzyme |
| clr | Centered-log ratio |
| CMD | Climatic moisture deficit |
| DNA | Deoxyribonucleic acid |
| DBH | Diameter at breast height |
| DSE | Dark septate endophyte |
| ITS | Internal transcribed spacer |
| K | Potassium |
| OTU | Operational taxonomic unit |
| MAP | Mean annual precipitation |
| MAT | Mean annual temperature |
| Mg | Magnesium |
| OG | Orthologous gene |
| N | Nitrogen |
| PERMANOVA | Permutational multivariate analysis of variance |
| PCR | Polymerase chain reaction |
| rRNA | Ribosomal ribonucleic acid |
| SEM | Structural equation modeling |

# 1. Introduction

Forests and woodlands cover roughly one-third of the global land surface area and support a multitude of organisms through their role in the cycling of carbon (C), water, and nutrients (Crowther et al. 2015a; Keenan et al. 2015). Trees, and plants in general, rely heavily on interactions with other organisms. Most of these interactions involve microorganisms, primarily bacteria and fungi, which inhabit leaves through to roots (Turner et al. 2013) and reach their highest diversity and biomass in soil (Baldrian, 2017). Soil microbes and their interactions play a central role in the cycling of C and nutrients, as well as influencing population and community dynamics and the productivity of plants (Van Der Heijden et al. 2008; Baldrian, 2017; Tedersoo et al. 2020).

The interactions occurring between plants and microorganisms span the spectrum from mutualism to commensalism, competition, and parasitism. On the continuum from plant to soil, i.e., plant-soil systems, some of the most widespread, integrated, and biologically important interactions occur between plants and their root symbionts—primarily mycorrhizal fungi (Smith & Read, 2010; Brundrett & Tedersoo, 2018). These mycorrhizal symbioses potentially mediate a substantial proportion of the photosynthetically fixed C that flows through roots to soil and nutrients that flow from soil up through roots during the exchange of these resources between symbiotic partners (Tedersoo & Bahram, 2019).

There has been a long-standing and growing interest in the way different types of mycorrhizal associations—mainly arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) associations—influence wide ranging ecological and biogeochemical processes, from C and nutrient cycling to plant-soil feedback, and biogeographical and evolutionary dynamics (Read, 1991; Phillips et al. 2013; Bennett et al. 2017; Brundrett & Tedersoo, 2018; Averill et al. 2019; Steidinger et al. 2019; Tedersoo et al. 2020). While generally inferred, less attention has been paid to exactly how these different mycorrhizal systems influence the broader microbial communities that they interact with, which is integral to understanding the processes that microorganisms facilitate.

In this thesis, through the lens of biotic interactions, I first consider the potential interactions occurring between mycorrhizal systems and soil organisms at large. I then address how mycorrhizal type may explain soil microbiomes on the level of vegetation communities at the regional scale. I follow this by addressing the extent to which colonization rates of different mycorrhizal and root-associated fungi may explain the root and soil microbiomes of widespread tree species across their latitudinal range. Lastly, I examine how leaf element and leaf-associated microbiome properties are explained by tree species and their nutrient-acquisition strategies via root symbioses, along with soil, climate, and geography. Overall, this thesis contributes to the understanding of the role of root symbioses in plant-soil system functioning pertaining to microbiomes and biotic interactions.

## 1.1 Plant-soil systems: Integrating above- and below-ground perspectives

From a global perspective, forests are typically classified into the four major biomes of boreal, temperate, sub-tropical, and tropical (Keenan et al. 2015), all with distinct climates, ecological communities, and C, water, and nutrient cycling regimes. Driven by large-scale differences in climate, there is generally a spectrum of rapid C and nutrient cycling and high aboveground C stocks in tropical forests, through to more conservative and slower C and nutrient cycling and high soil C stocks in boreal forests, with temperate forests somewhere in between; furthermore, tropical forests tend to be phosphorus (P) limited and boreal forests tend to be nitrogen (N) limited (Vitousek et al. 2010; Scharlemann et al. 2014; Crowther et al. 2015a; Gill & Finzi, 2016; Steidinger et al. 2019).

The trees, and plants in general, growing in forests possess a variety of functional traits associated with balancing growth, survival, and reproduction (Díaz et al. 2016). These traits can be considered within a plant-economic trait spectrum that encapsulates a gradient of slow and conservative mechanisms through to fast and acquisitive mechanisms of resource use and investment (Reich, 2014). Compared to slow and conservative plants, fast and acquisitive plants tend to invest more in growth than survival, which corresponds to less structural C investment and higher biomass turnover, hydraulic conductivity, photosynthetic capacity, respiration, and N and P tissue concentrations (Wright et al. 2004; Reich, 2014; Lambers & Oliveira, 2019; Luo et al. 2021).

Within woody plants, the major differences in functional traits are seen between gymnosperms (conifers) and angiosperms (broadleaves) (Díaz et al. 2016), which have been considered to represent a fast (angiosperm) versus slow (gymnosperm) trait tradeoff (Bond, 1989; Brodribb et al. 2012). Accordingly, angiosperms tend to outcompete gymnosperms and dominate most tropical and temperate forests, while gymnosperms tend to dominate in colder climates and on nutrient poor soils (Bond, 1989; Reich, 2014). Yet both angiosperms and gymnosperms persist in all forest biomes (Brodribb et al. 2012). Furthermore, both gymnosperms and angiosperms can have evergreen and deciduous foliage—a further divide of fast (deciduous) and slow (evergreen) traits—although the deciduous habit is more common in angiosperms and the evergreen habit is more common in gymnosperms (Gower & Richards, 1990; Reich & Bolstad, 2001).

Regarding roots, the one-dimensional fast versus slow ecological trait tradeoff has been questioned. Roots appear to be multidimensional in their economic traits and not analogous nor coordinated with leaf traits, especially for woody plants (Weemstra et al. 2016). A misalignment of root traits is in those generally associated with root lifespan (Kramer-Walter et al. 2016; Kong et al. 2019). The multidimensional root-trait space has been associated with an additional fungal collaboration gradient ranging from outsourcing resource acquisition to mycorrhizal fungi on one extreme to direct root resource acquisition on the other extreme (Weemstra et al. 2016; Bergmann et al. 2020). It becomes much more complicated for woody plants when considering different mycorrhizal types, which further alter root traits likely due to differences in the physical properties and ecology of these different root symbioses (Kong et al. 2019). Yet, when considering AM and EcM imprints in aboveground economic traits of woody plants, they tend to contribute to the fast-slow trait spectrum (Averill et al. 2019). This highlights the great importance of considering root symbioses, leaf habit and phylogeny, and climatic biomes when assessing plant-soil system functioning.

## 1.2 Mycorrhizal symbioses

While there are several types of mycorrhizal symbioses, the dominant types are EcM and AM associations in terms of geographical distribution and number of tree species involved (Brundrett & Tedersoo, 2018; Steidinger et al. 2019). Mycorrhizal associations are not merely an extension of plant root systems, they involve species of both plants and fungi, and accordingly, there are great differences both between and within AM and

EcM fungi according to their morphological, physiological, ecological, and phylogenetic properties (Tedersoo & Bahram, 2019).

### *Evolutionary and phylogenetic perspectives*

The AM symbiosis is formed between 250–1,000 species of obligately symbiotic fungi—from the sub-phylum Glomeromycotina (or phylum Glomeromycota) within Mucromycota (Kivlin et al. 2011; Öpik et al. 2013; Spatafora et al. 2016)—and around 72% of terrestrial plants (ca. 200,000 species) across a broad phylogeny, including Bryophytes, Pteriophytes, Gymnosperms, and Angiosperms (Brundrett & Tedersoo, 2018). The AM symbiosis is thought to have evolved alongside the terrestrialization of plants some 400–450 million years ago, having undergone few evolutionary changes since, apart from the gain and loss of hosts (Bidartondo et al. 2011; Choi et al. 2018). In comparison, the EcM symbiosis involves over 20,000 fungal species, mainly from the phyla Basidiomycota and Ascomycota (Rinaldi et al. 2008), and around 2% of plant species, almost exclusively limited to woody gymnosperms and angiosperms (Brundrett & Tedersoo, 2018). The EcM symbiosis has evolved multiple times—first appearing around 200 million years ago—across 80 different fungal clades from functionally diverse saprotrophic ancestors (Tedersoo & Bahram, 2019; Miyauchi et al. 2020; Ryberg et al. 2022). The evolutionary convergence of EcM symbioses—apart from acquiring genes involved in the formation of symbiosis—has generally involved the loss of genes encoding plant cell wall degrading enzymes, although certain taxa have retained unique sets of such enzymes, leading to a functionally diverse symbiosis (Kohler et al. 2015; Miyauchi et al. 2020).

### *Structural properties of the symbioses*

The defining feature of AM symbioses are highly branched intracellular hyphal structures called arbuscules that form in the inner root cells, and the cells they colonize represent the site of active nutrient and water exchange (Bonfante & Genre, 2010). The EcM symbiosis, on the other hand, is characterized by the formation of modified lateral root branching with short terminal root tips. These root tips are covered in a fungal hyphal sheath called the mantle, and within the roots an intercellular Hartig net is formed and is considered the site of nutrient and water exchange (Taylor & Alexander, 2005; Bonfante & Genre, 2010). Apart from arbuscules, AM fungi—with several morphological variations—also form intracellular, intercellular, and extracellular (extraradical) hyphae, large asexual spores, and some taxa form lipid-rich vesicles, which are thought to function as an energy reserve (Harrison, 1999; Dickson et al.

2007). Most AM structures, apart from spores, are ephemeral, likely lasting several days to several weeks, representing a high turnover of biomass (Staddon et al. 2003; Pepe et al. 2018). In terms of extraradical mycelia, EcM fungi tend to form distinct morphological exploration types. With several variations, these exploration types range from contact types with smooth mantles and few emanating hyphae to short and medium-distance types with extensive emanating hyphae and long-distance types with few aggregate mycelial cords or rhizomorphs (Agerer, 2001). As their mycelia range from hydrophilic (contact, short, and medium-smooth types) to hydrophobic (other medium and long-distance types), the exploration type has been used to infer physiological and functional variation in EcM associations, specifically relating to inorganic and organic N acquisition (Hobbie & Agerer, 2009) and water acquisition (Lehto & Zwiazek, 2011). Furthermore, EcM structures can be persistent, with turnover times ranging from weeks to months and potentially years (Finlay & Read, 1986; Ekblad et al. 2013). Overall, EcM associations have a greater physical presence on the roots, and AM associations can have a greater presence inside the roots.

### *Role of the symbioses in plant function*

The primary function of both symbioses is thought to be the exchange of C and nutrients between the host plant and fungus. The major nutrients obtained through AM fungi and their high hyphal surface area are generally inorganic phosphorus (P) followed by inorganic nitrogen (N) (Smith & Smith, 2011). Functionally, EcM associations also play a role in plant N and P acquisition, both inorganic and organic, depending on the fungal taxa involved—and exploration types—and their ability to decompose organic matter, a capacity that is completely lacking in AM fungi (Tedersoo & Bahram, 2019). Plants, in return, may provide their EcM partners with up to 30% of their photosynthates, compared to up to 20%—and usually less—allocated to AM partners (Leake et al. 2004).

Apart from nutrient acquisition, AM and EcM associations may also, to varying degrees, confer resistance against pathogen and herbivore attack, improve drought, salinity, and heavy metal tolerance, and contribute to soil aggregation (Marx, 1972; Johansson et al. 2008; Lehto & Zwiazek, 2011; Miransari, 2011; Veresoglou & Rillig, 2012; Chitarra et al. 2016; Tao et al. 2016; Lehmann et al. 2017). Yet, while AM fungi are generally considered to be mutualists or commensalists, under certain conditions they may act as parasites of the host plant (Smith & Smith, 2012; Bennett & Groten, 2022; Kaur et al. 2022). At least in some boreal forests, it has been suggested that EcM fungi—particularly taxa adept at accessing organic N—may lock their host into a N limitation feedback loop, further reinforcing the need for EcM associations in these ecosystems (Franklin et al. 2014). The root colonization rate by AM fungi appears to be highest under mild climates with high soil N availability, compared to EcM colonization, which tends to be higher under mesic climates with constant precipitation and in acidic soils (Soudzilovskaia et al. 2015). Overall, the major difference in functioning between EcM and AM symbioses when it comes to forests appears to be the organic N acquisition of some EcM fungi, which seemingly leads to a higher reliance of EcM trees on their EcM fungi. Compared to EcM trees, AM trees may be more flexible in terms of their nutrient-acquisition pathways and rely less on their AM fungi, i.e., a more flexible symbiosis.

### *Mycorrhizal type as a plant-soil system trait*

Early observations of the biogeographic patterns of different types of mycorrhizal associations showed that they were associated with distinct ecosystems and soil environments, with EcM found on trees in acidic soils with high litter accumulation and AM found on herbaceous and woody plants growing in soils with high mineral N availability (Read, 1991). This led to the idea that AM and EcM systems form distinct C and nutrient cycling syndromes, with plant-soil feedback enforcing fast-open nutrient economies in AM systems and slow-closed nutrient economies in EcM systems, known now as the mycorrhizal-nutrient economy (MANE) framework (Read & Perez-Moreno, 2003; Chapman et al. 2006; Phillips et al. 2013). A plethora of studies have since begun to unravel the scale and extent to which these mycorrhizal associations have influenced and influence evolutionary, ecological, and biogeochemical processes in vegetation communities.

Trees associating with EcM account for an estimated 60% of Earth's tree stems, dominating most temperate and boreal forests, compared to AM trees contributing most of the remaining 40% of tree stems, dominating mostly in tropical forests (Steidinger et al. 2019). In accordance, EcM vegetation biomass is positively correlated, and AM vegetation biomass tends to be negatively correlated with topsoil C content globally (Soudzilovskaia et al. 2019). Mycorrhizal type has further been shown to be linked to a suite of woody plant economic traits, with AM and EcM plants systematically differing in P and N economic traits, where EcM plants have more conservative traits in both cases, most evident in temperate forests (Averill et al. 2019). Additionally, differences in soil biogeochemical properties of AM and EcM forests have been observed across tropical forests, which have generally been neglected from investigations into the effect of the mycorrhizal type (Barceló et al. 2021). Even less evidence of mycorrhizal type effects has been observed in boreal forests, which is obviously challenging as AM trees are much less common, highlighting the intertwined nature of mycorrhizal type, plant phylogeny, and climate (Read, 1991; Brundrett & Tedersoo, 2018; Steidinger et al. 2019). A potential mechanism to further address differences in mycorrhizal type is to observe responses across tree species with EcM and AM associations that cover large environmental gradients and geographic distributions.

### *Other root associations on mycorrhizal trees*

Despite the general assignment of mycorrhizal type as a binary, some trees can form dual-mycorrhizal roots, i.e., EcM and AM associations simultaneously (Brundrett, 2006). These dual-mycorrhizal associations may be synergistic and confer on their host increased stress tolerance and flexible avenues of nutrient acquisition, and thus present a unique system to compare mycorrhizal types (Teste et al. 2020). In addition, some tree species also form N-fixing symbioses with actinorhizal or rhizobial bacteria, which can fix atmospheric $N_2$ and represent a significant input of N into the soil system (Amundson et al. 2003; Wang et al. 2010). These trees tend to be concentrated mostly in the tropical and southern latitudes (Steidinger, 2019), yet actinorhizal trees become more common northward and are typically obligated to their N-fixing symbiosis that maintains N fixation regardless of soil N status (Menge et al. 2014). Nitrogen-fixing trees generally also form mycorrhizal associations with either EcM, AM, or both (Gardner, 1986; Brundrett &Tedersoo, 2018). The interaction between N-fixing and mycorrhizal symbioses is of great interest yet still poorly understood, as single symbionts are generally studied in isolation. Some evidence suggests that the presence of mycorrhizal fungi can stimulate N fixation (Yamanaka et al. 2003), and EcM fungi on N-fixing trees may be associated with enhanced P acquisition abilities (Walker et al. 2014).

Tree roots can also be colonized by different endophytic fungi to varying degrees. Of these, dark septate endophytic (DSE) fungi appear to be facultative, host generalists, common, and extensive colonizers of root systems across many different hosts and ecosystems (Mandyam, 2005). Dark septate endophytes—defined as fungi with melanized septate hyphae that colonize living plant roots—are an enigmatic and varied group of ascomycetous fungi whose ecological functions are poorly understood. They possibly act on a spectrum between free-living saprotrophs, mycorrhizal fungi, and parasites (Ruotsalainen et al. 2021). Yet, they have also been linked to enhanced access to nutrients and protecting against pathogens, which improve plant performance in harsh and stressful conditions (Newsham et al. 2011; Santos et al. 2021). Many endophytic fungi, including DSE, fungi capable of forming ericoid mycorrhiza, and known saprotrophs, appear to be prominent in EcM-colonized root tips (Pellitier & Zak, 2021). Such root-associated fungi can also occur in the roots of both EcM and AM trees in the same forest (Toju & Sato, 2018), though their function in these contexts is unknown. Clearly, there remains plenty of work to do to unravel the complex nature of root associations and their potential effects on plant performance, soil microbiomes, and ecosystem functioning.

## 1.3 Microbial communities in mycorrhizal systems

Microorganisms, ranging from prokaryotic bacteria and archaea to eukaryotic protists and non-mycorrhizal fungi, contribute to the proposed nutrient economies of EcM and AM systems. Multiple mechanisms have evolved in plants to modify the composition of microbial communities for their benefit (Vandenkoornhuyse et al. 2015; Rebolleda-Gómez & Ashman, 2019). In return, these microorganisms regulate plant health and productivity throughout terrestrial ecosystems (Van Der Heijden et al. 2008). The community structure of these organisms and their interactions are differentially influenced by abiotic factors such as climate and soil pH (Fierer, 2017). Free-living fungal saprotrophs are the primary decomposers of organic matter (Treseder & Lennon, 2015), and some fungi are also among the most destructive plant pathogens (Fisher et al. 2012). Bacteria are responsible for a multitude of nutrient transformations in soils. They also play a complementary role to fungi in the decomposition of organic matter and are important symbionts in plants, animals, and fungi (Fierer, 2017; Husnik & McCutcheon, 2018; López-Mondéjar et al. 2020). Accumulating evidence suggests that biotic interactions such as facilitation and metabolic cross-feeding (i.e., microbes further metabolizing the metabolites of other microbes), resource and niche competition, and predation may mediate microbiome function and hence microbial control of ecosystem functions (Crowther et al., 2015b; Bahram et al. 2018; Koltz et al., 2018; Geisen et al. 2020; Albright et al. 2022). Cooperative (metabolic cross-feeding) interactions appear to predominate in bacterial communities, especially in host-associated as opposed to environmental habitats (Machado et al. 2021). Moreover, fungi with their mycelial habit are more resistant to extreme conditions than bacteria, yet they can aid bacteria by connecting resource-rich patches and degrading recalcitrant C, which can provide bacteria with labile C (Carreira et al. 2020; Bahram & Netherway, 2022).

As a bridge between plant and soil, mycorrhizal symbioses mediate interactions between plant and soil microbiomes. Consequently, AM and EcM systems can host contrasting microbial communities due to direct interactions and indirectly by their contrasting soil nutrient syndromes (Phillips et al. 2013; Tedersoo & Bahram, 2019). Both AM and EcM fungi can select for distinct bacterial communities around their extraradical hyphae, presumably via hyphal exudation and other mechanisms (Kluber et al. 2011; Emmett et al. 2021; Zhang et al. 2021). By contributing to unfavorable acidic and low-nutrient soil conditions, EcM mycelium can have antagonistic effects on free-living microbial guilds in the soil (Frey, 2019; Tedersoo & Bahram, 2019).

Overall, EcM fungi may more efficiently take up nutrients and immobilize nitrogen than AM fungi and have a greater physical presence in the soil and on roots, resulting in more direct microbial interactions, and thus may have a greater impact on the soil microbiome than AM fungi. However, little is known about the role of DSE and other root-associated microbes in these dynamics. Due to their high diversity and an often-uncultivatable nature, forest microorganisms were largely unknown until relatively recently. The recent rapid development of high-throughput sequencing methods permits unprecedented direct determination of the genetic content of samples for species and functional gene identifications (Nilsson et al. 2019), which can facilitate a rapid advancement in our knowledge of plant-microbial interactions.

# 2. Objectives

The purpose of my thesis was to increase our understanding of how plants and their root symbioses, particularly in forests, influence the structure and function of belowground microbiomes and how they also influence leaf element profiles and leaf microbiomes. Thus, I addressed the following fundamental questions:

(1) What are the major interactions occurring between root-symbiotic fungi and belowground microbiomes? (**Papers I**, **II**, & **III**)
(2) How does the dominant mycorrhizal type (AM and EcM) of vegetation communities determine the structure and potential function of soil microbiomes? (**Papers I & II**)
(3) How does the level of root colonization by EcM, AM, and DSE fungi across widespread deciduous broadleaved trees affect the structure and potential function of associated root and soil microbiomes across Europe (**Paper III**)
(4) How do tree species and their nutrient-acquisition strategies via root symbioses influence their leaf element properties and associated microbiomes across Europe? (**Paper IV**)

# 3. Methods

## 3.1 The study sites and tree species

For **Paper I**, all climatic forest biomes are considered; however, the reviewed studies mostly come from the Northern Hemisphere and specifically temperate and boreal forests. The data used for **Paper II** comes from 145 sites with various vegetation and soil types across the northern Baltic region in Estonia and Latvia (Figure 1), with little climatic variability (4.7–7.0°C MAT and 549–745 mm MAP). The vegetation types considered were EcM forests (coniferous, deciduous, or N fixing), AM forests (coniferous or deciduous), AM croplands, and AM grasslands, which were assigned based on the relative basal area (trees) or relative cover (grasses and crops); in total, 73 woody species were included.

The data used for **Papers III** and **IV** comes from 30 plots spread across 18 sites covering a 3 220 km latitudinal gradient from northern Norway to central Italy (Fig 2), with a climatic range of 0.8–15.1°C MAT and 486–1,213 mm MAP. Sites were generally EcM-dominated mixed forests (60–95% relative basal area) and most of them were situated in vegetation reserves or close to research stations. Across the sites, six tree species (*Alnus glutinosa, A. incana, Betula pendula, Sorbus aucuparia, S. domestica,* and *S. torminalis*) from three genera were sampled. Tree species were chosen due to their widespread distributions, common leaf habit (deciduous broadleaf), and preferences for different mycorrhizal types and N-fixing ability (*Alnus* = EcM/AM and N-fixing, *Betula* = EcM, and *Sorbus* = AM) according to the FungalRoot database (Soudzilovskaia et al. 2020).

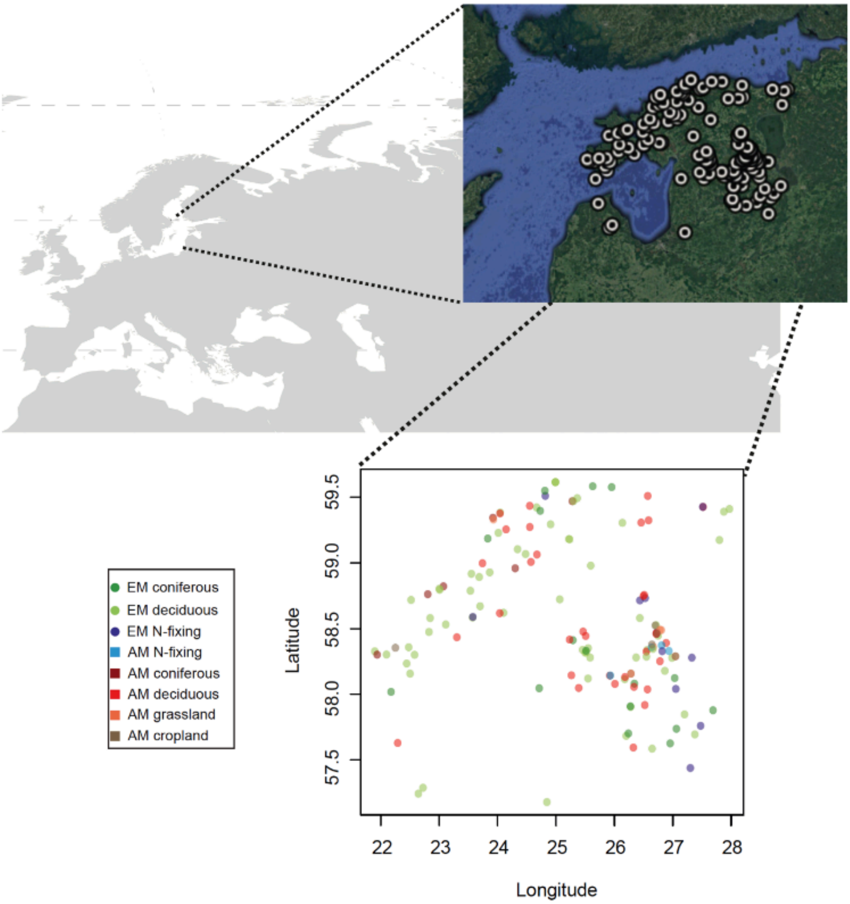

Figure 1. The location of sampling sites used in **Paper II** from Estonia and Latvia in the Northern Baltic Region, and the distribution of sites in terms of their longitude, latitude, and dominant vegetation type (Reproduced from **Paper II**; Bahram et al. 2020 with permission from the publisher).

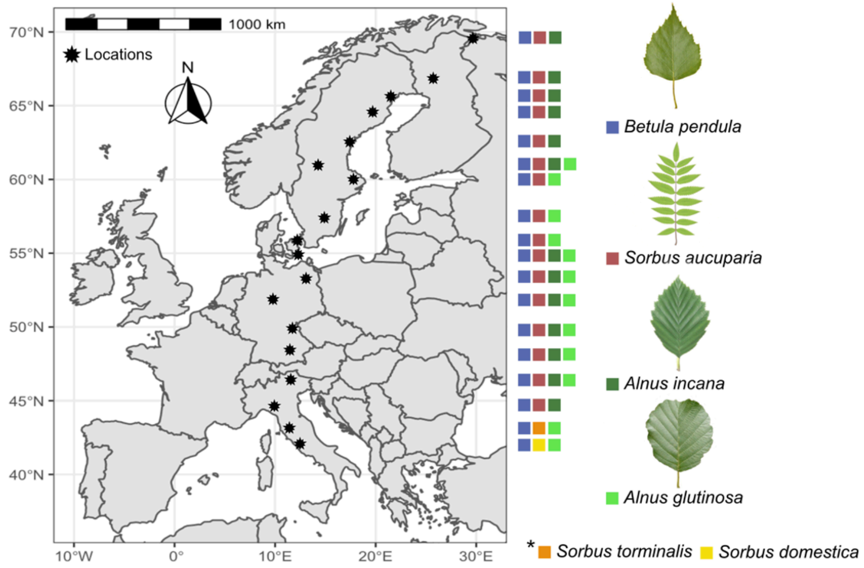

Figure 2. The location of sampling sites used in **Papers III** and **IV** from northern Norway to central Italy, and the presence of the sampled tree species at each site (Reproduced from **Paper III**).

## 3.2 Sampling method

For **Paper I**, the literature on EcM and AM fungi, trees, and forests was reviewed, with a particular focus on the literature exploring the interactions between AM and EcM systems with saprotrophs, soil grazers, predators, and N-cycling microorganisms. For **Paper II**, sampling occurred primarily during the growing season between 2011 and 2016; at each site, a 2,500 m2 plot was established, and 40 soil sub-samples (5 cm in diameter and 5 cm in depth) were collected without separating organic and mineral soil. The 40 soil sub-samples per plot were then combined to create a composite sample, which was homogenized and air-dried within 12 hours of collection.

For **Papers III** and **IV**, sampling was undertaken between the 5th of August and the 11th of September 2019 in a north-to-south direction to avoid major differences in the stage of the growing season. At each site, five individual trees of each target species present were selected that were at least 10 m apart and had a diameter at breast height (DBH) of 10–20 cm;

this totaled to 305 individual sampled trees across the 18 sites. If the different tree species were not growing in the same vegetation communities at the same site, they were considered separate plots, resulting in a total of 30 plots.

For each individual tree, four soil samples (5 cm diameter x 10 cm depth; no separation of mineral and organic layers) were taken from each cardinal direction 50 cm from the base of the tree after removing loose litter and pooled to form one composite sample per tree species per site and homogenized. On the same trees, fine root samples were taken from the top 10 cm of soil (same individual points as soil samples) by tracing them to the major lateral roots of the target tree. They were then gently shaken and rinsed in water before being stored in 70% ethanol until further analysis. Also, on the same trees as above, approximately 30 leaves were collected from a 50 x 50 x 50 cm area of the mid-canopy using extendable loppers. All soil and leaf samples were air-dried within 12 hours of collection.

Additionally, according to a modified version of the Teabag Index protocol (Keuskamp et al. 2013), a Lipton teabag with rooibos (C:N = 43) and one with green tea (C:N = 12) were buried to 10 cm deep at each tree. They were collected after 12 months at 10 sites (only those accessible owing to Covid-19 related travel restrictions) from Norway to Germany. In total 284 of 330 teabags were recovered from these sites (at least three replicates per species per site) and dried at 70°C until a constant weight was achieved to measure mass loss.

## 3.3 Soil, leaf, vegetation, and climatic variables

For **Papers II**, **III**, and **IV,** soil $^{13}$C and $^{15}$N natural abundances and total soil C and N contents were determined with an isotope ratio mass spectrometer and elemental analyzer; the same analysis was performed on leaf samples in **Paper IV**. Soil pH, extractable phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and leaf P, K, Ca, and Mg concentrations were measured using standard methods. For **Paper III** and **IV,** gravimetric moisture content was measured from a sub-sample of moist field soil that was oven dried until a constant weight was achieved.

Climate data was obtained based on geographic coordinates and downloaded from the WorldClim database (www.worldclim.org) (**Paper II**) or CHELSA V2.1 (Karger et al. 2017) (**Papers III** and **IV**). Climatic moisture deficit (CMD)—the difference between atmospheric evaporative demand and precipitation—was obtained from INDECIS (www.indecis.csic.es). Modeled annual atmospheric N deposition data (**Paper IV**) for the year 2019 was obtained from EMEP via the Norwegian

Meteorological Institute (www.emep.int). For all plots (2500 m$^2$) in **Papers II**, **III**, and **IV**, vegetation community variables were obtained by recording all present tree species and measuring their DBH to obtain their relative basal area.

## 3.4 Root-symbiont colonization analysis

For **Papers III** and **IV,** the root colonization rate (% root tips colonized) by EcM fungi was assessed on all *Betula* and *Alnus* fine root samples under a dissecting microscope at 20X magnification. Cleaned roots were cut into 1-cm pieces (totaling around 20 cm), spread randomly in a petri dish with water, and a total of 100 tips were scored as colonized if a mantle was present (swollen short-root tips covered in hyphae with root hairs absent) or uncolonized if one was not present. The root colonization rate (% root length colonized) by AM and DSE fungi was assessed on all *Alnus* and *Sorbus* fine root samples by the grid line intersection method (McGonigle et al. 1990) using 1 cm pieces of cleaned roots (around 10 cm total), cleared in 2.5% KOH solution, and stained with trypan blue in an acidic glycerol solution (Koske & Gemma, 1989). Stained roots were mounted on slides in acidic glycerol, and on a minimum of 100 random fields of intersection at 40X magnification, the presence of arbuscles, hyphae, and vesicles (if present) of AM fungi and the presence of dark-septate hyphae of DSE were counted.

## 3.5 Metabarcoding of bacterial and fungal communities

The extraction of DNA from dried and pulverized soil, root, and leaf samples was performed using standard kits according to their instructions. Across all samples, Bacteria (and Archaea) were amplified using polymerase chain reaction (PCR) with the primers 515FB and 926R to target the ribosomal rRNA 16S gene V4–V5 regions (Walters et al. 2016) and sequenced on the Illumina HiSeq and NovoSeq platforms. For **Paper II**, soil fungi (and eukaryotes in general) were PCR amplified with the primers ITS9MUNngs and ITS4ngsUni (Tedersoo & Lindahl, 2016) targeting the partial 18S rRNA gene (V9 subregion) and full-length internal transcribed spacer (ITS) region and sequenced using the PacBio platform. For **Paper III,** soil and root fungi were PCR amplified using variations of the gITS7 and ITS4 primers (Ihrmark et al. 2012; Tedersoo & Lindahl, 2016) and sequenced on the Illumina NovoSeq platform. And leaf fungi in **Paper IV** were PCR amplified using the primers ITS1catta and ITS4ngsUni (Tedersoo & Anslan, 2019), and sequenced on the PacBio platform. Sequencing from PacBio gives longer reads, while Illumina gives higher throughput and sequencing depth (Tedersoo et al. 2018), and they both appear to reveal similar patterns in the structure of fungal communities (Furneaux et al. 2021).

All 16S amplicon and ITS amplicon sequences from **Papers III** and **IV** were processed using the LotuS2 pipeline (LotuS1 for **Paper II**) (Özkurt et al. 2022), and the PipeCraft pipeline (Anslan et al. 2017) was used for ITS amplicons in **Paper II**. Chimeras were removed, and all sequences were clustered into operational taxonomic units (OTUs) with a 97% similarity threshold, and taxonomy was assigned against the SILVA and UNITE databases for prokaryotic and eukaryotic sequences, respectively. All non-target taxonomic groups were removed from both the 16S and ITS datasets. Fungi were further assigned lifestyles at the genus level based on various databases (Nguyen et al. 2016; Põlme et al. 2020), or further curated based on lifestyle flexibility, growth habits, and different habitats.

## 3.6 Shotgun metagenomics of roots and soils

All DNA samples from **Paper I** and pooled root and soil samples from **Papers III** and **IV** that passed quality checks were subjected to shotgun metagenomic sequencing on the Illumina HiSeq (**Paper I**) and NovaSeq (**Papers III** and **IV**) platforms. Metagenomic bioinformatic analysis was performed using the MATAFILER pipeline (Hildebrand *et al.* 2021) following the strategy developed in Bahram et al. (2018). Reads were quality filtered, trimmed, and merged, followed by a similarity search approach using DIAMOND (Buchfink et al. 2015) to estimate the functional gene composition of each sample. The abundances of orthologous gene (OG) groups were obtained by mapping reads against the eggnog database (Huerta-Cepas et al. 2019), the KEGG database (Kanehisa & Goto, 2000), and, for carbohydrate-active enzyme (CAZyme) annotations, reads were mapped against the CAZy database (Cantarel et al. 2009). For **Papers III** and **IV**, based on KEGG IDs, N cycling gene annotations were obtained from the NCycDB database (Tu et al. 2019) and P cycling gene annotations were obtained from the PCycDB database (Zeng et al. 2022). For databases that included taxonomic information, reads were mapped and assigned to prokaryotic and eukaryotic groups. Furthermore, the metagenomic relative abundance of bacteria and fungi based on small subunit (SSU) rRNA genes was calculated (Logares et al. 2014).

## 3.7 Data analysis

Data management, statistical analyses, and data visualizations were done using the RStudio platform unless otherwise stated. For **Paper II**, residuals of models with the square root of total read abundance were used for analyzing OTU and gene count matrices. For **Papers III** and **IV** OTU count matrices were centered-log ratio (*clr*) transformed with an added pseudo-count, which gives the proportional abundance relative to the sample geometric mean and accounts for the compositional nature of the data (Gloor et al. 2017). Gene count matrices were normalized as a percentage of the total number of reads used for mapping, accounting for differences in library size and including the fraction of unmapped (functionally unclassified) reads (Bahram et al. 2018). Analyses in **Papers III** and **IV** were performed on the level of tree species per site, where group means were used for root and soil communities and leaf element properties (dry mass concentrations), compared to group composite values that were used for leaf communities and soil and root functional genes. Richness was used for the analysis of the alpha diversity of taxa and guilds and genes in **Paper II**, and the Shannon diversity (H) index, which accounts for both richness and relative abundances, was used for the alpha diversity of taxa, guilds, and genes in **Papers III** and **IV** and was calculated using the *vegan* package (Oksanen et al. 2019).

To examine univariate relationships between variables, nonparametric Spearman's rank correlation coefficient analyses were performed. For further analyses, the best predictor variables were identified using a model selection procedure based on a machine learning approach in the *Randomforest* package (Liaw & Wiener, 2002). To test direct relationships between variables of interest, either simple linear models (**Paper IV**) or linear mixed-effects models (**Papers III** and **IV**) were fitted using the *lme4* (Bates et al. 2009) and *nlme* (Pinheiro et al. 2017) packages, with plot embedded in site (**Papers III**), or additionally crossed with tree species (**Paper IV**) as random effects structures. The marginal and conditional $r^2$ were calculated using the *MuMln* package, *p*-values were calculated using the *lmerTest* package (Kuznetsova & Brockhoff, 2017), and model fit was evaluated based on the Akaike information criterion (AIC), marginal $r^2$ values of the fixed effect, *p*-values, and standardized model residuals.

To further test the direct and indirect effects of variables, we built structural equation modeling (SEM) models in the AMOS software (SPSS) in **Paper II** or the *PiecewiseSEM* package (Lefcheck, 2016) in **Paper III** to account for random effect structures. In a prior model, all indirect and direct links between variables were established based on their correlations. Differences between the relative abundance of the main taxonomic and functional groups across different categories of a response variable (e.g., mycorrhizal type) were tested using a non-parametric Wilcoxon rank-sum test with Benjamini-Hochberg multiple testing correction (**Paper II**), and the same analysis was performed in **Paper IV** on pairwise comparisons between tree species across their overlapping sites.

For multivariate analysis of microbial communities and functional gene compositions, as well as leaf nutrient profiles, permutational multivariate analysis of variance (PERMANOVA) with 999 permutations was performed using the *adonis* function of the *vegan* package. For this analysis, the Bray-Curtis dissimilarity was calculated between each pair of samples (**Paper II**, and functional genes in **Paper III**), and Euclidean distances for *clr*-transformed community matrices in **Papers III** and **IV** and biotic and abiotic explanatory variables were forward selected using the *forward.sel* function of the *adespatial* package (Dray et al. 2018). To analyze shared and unique variation in leaf bacterial and fungal community composition (**Paper IV**) as explained by vegetation (tree species, EcM tree basal area, coniferous EcM tree basal area, and tree diversity), leaf element properties (concentrations, stoichiometry, and stable isotope compositions), climate/geography (MAT, MAP, CMD, N deposition, and altitude), and spatial structures (principal coordinates of neighbor matrices PCNM; calculated from latitude and longitude); variation partitioning analysis was performed using the *varpart* function of the *vegan* package on forward selected variables using the *forward.sel* function of the *adespatial* package.

To visualize and analyze differences in leaf element profiles and leaf bacterial and fungal communities across tree species (**Paper IV**), I performed principal component analysis (PCA), using Euclidean distances of *clr*-transformed microbial data, and calculated the importance of explanatory variables using the *envfit* function with 999 permutations in the *vegan* package.

# 4. Results and discussion

## 4.1 The importance of biotic interactions in mycorrhizal systems

In **Paper I**, I explored the plethora of potential interactions occurring between EcM and AM systems with soil organisms by reviewing the literature. In line with previous observations, climate and tree traits such as deciduous or evergreen, together with mycorrhizal type, lead to the formation of plant-soil systems with distinct nutrient cycling syndromes reliant on the outcome of interactions with soil organisms (Figure 3). The slow and closed organic nutrient cycle suggested for EcM systems (Phillips et al. 2013), which is mainly evident in cold-climate coniferous EcM forests (Read, 1991), and appears to be strongly related to EcM fungi under limited N conditions (Högberg et al. 2017). These EcM fungi are likely the dominant soil organisms in these soils and promote a soil community with low-functional redundancy that reinforces inorganic nutrient-poor systems via control of soil pH and C:N (Figure 3b). In comparison, the open and rapid inorganic nutrient cycle suggested for AM systems is mainly evident in broadleaf forests of milder and warmer climates (Phillip et al. 2013), which may have more diverse and functionally redundant soil communities with more competitive and antagonistic interactions, i.e., a higher prevalence of saprotrophs, plant pathogens, and nutrient-transforming microbes (Figure 3b).

This suggests that EcM and AM systems may respond differently to environmental change, including climate change, where AM systems may be more resilient while the functioning of EcM systems may be impaired under higher nutrient availability, and under warmer and drier climates (Fernandez et al. 2017; Jo et al. 2019; Pugnaire et al. 2019; DeForest & Snell, 2020), likely due to their unique C and nutrient syndromes generated by tree, mycorrhizal, and soil organism interactions.

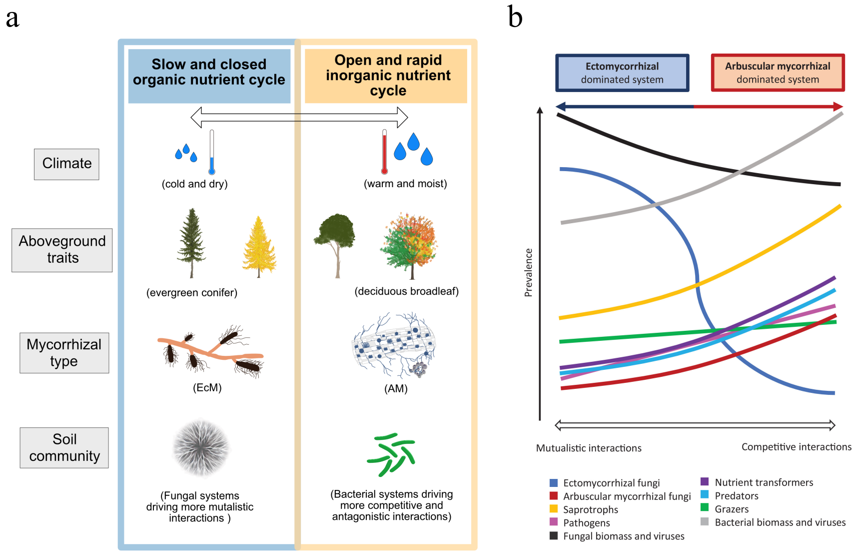

Figure 3. Conceptual figure of the main ideas reviewed in **paper I**, showing (a) the alignment of properties that are proposed to lead to slow and closed organic nutrient cycles and open and rapid inorganic nutrient cycles in AM and EcM systems, respectively, by driving biotic interactions in the soil, and (b) the proposed biotic interactions and soil guilds that shift from EcM dominated systems to AM dominated systems (modified from **Paper I**; Netherway et al. 2021).

## 4.2 The structure and function of soil microbiomes in EcM and AM systems

Building on the hypotheses formed in **Paper I**, **Paper II** shows that soil microbiomes in habitats dominated by vegetation with different root symbioses, especially mycorrhizal types, have contrasting microbial communities (Figure 4).

Vegetation communities dominated by AM associations had higher relative abundances of non-fungal eukaryotes and saprotrophic fungi compared to EcM-dominated habitats (Figure 4a); this is consistent with higher decomposition rates in AM systems (Tedersoo & Bahram, 2019) and suggests that EcM fungi may compete with free-living saprotrophs (Bödeker et al. 2016), bacteria, and other soil microbes for N resources, which were negatively correlated with increasing EcM dominance (Figure 4a & b). Increasing dominance of coniferous EcM plants appeared to be a driver of increased soil C:N ratios and decreased soil pH, which reduced the richness of bacteria, archaea, protists, and the bacteria:fungi abundance ratio (Figure 4 a & b). Soil pH is known to be a strong determinant of bacterial communities and their richness (Rousk et al. 2010; Bahram et al. 2018). The activity of bacteria, especially in decomposition, is enhanced under high pH and a low C:N ratio compared to fungi due to physiological differences including pH-related stress tolerance and elemental stoichiometry (Rousk et al. 2010; Waring et al. 2013; Bahram et al. 2018). Furthermore, AM vegetation was associated with relatively more putative plant pathogenic fungi, especially with increasing deciduous AM trees (Figure 4a); this is in line with other evidence suggesting AM trees experience more antagonistic interactions with their associated soil microbes compared with EM trees (Bennett et al. 2017; Teste et al. 2017; Kadowaki et al. 2018), as EcM fungi may form a physically more protective barrier to pathogens (Branzanti et al. 1999; Kadowaki et al. 2018) and overall reinforce more unfavorable soil conditions for antagonistic organisms.

While these results presented here suggest overall differences in soil microbiota between EcM and AM systems, there are also differences within mycorrhizal types, such as between deciduous and coniferous EcM-dominated habitats, indicating that mycorrhizal type effects may depend greatly on other vegetation factors such as phylogeny or leaf habit (broadleaf vs. coniferous).

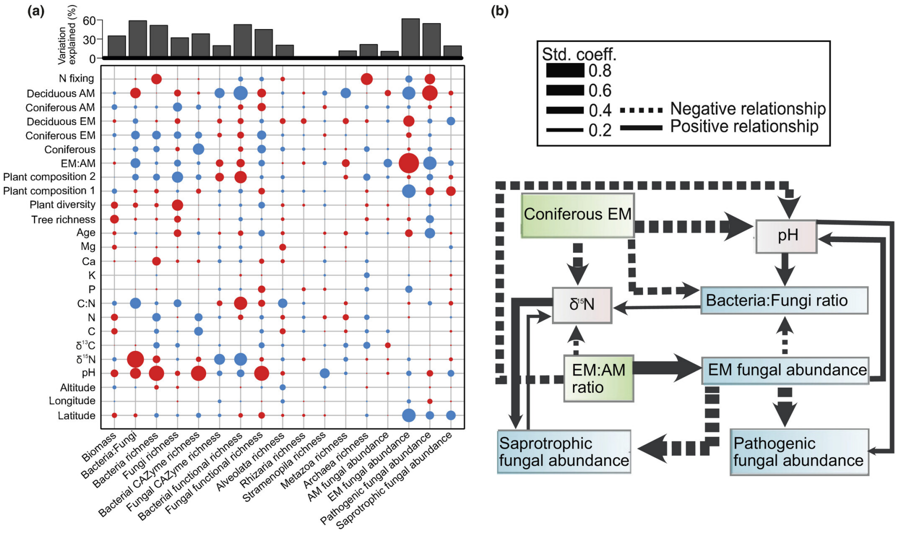

Figure 4. The main findings from **Paper II** on microbial diversity and composition. (a) Random Forest heatmap indicates relationship of microbial taxa and functional groups to plant traits, edaphic and geographical variables. The size of circles corresponds to the variable importance (% of mean decrease accuracy); blue and red depict negative and positive Spearman correlations, respectively. Plant composition 1 and 2 are the first two principal components analysis (PCA) axes representing changes in the composition of plants across the plots. The top barplot shows the variance explained for each model with the dependent variables on the *x*-axis. (b) Best-fitting structural equation model based on relationships retrieved in (a) for the relative abundance of bacteria and fungi. All relationships were significant ($P < 0.05$) and model fits were acceptable according to chi-square test ($P > 0.1$) and PCLOSE test ($P > 0.1$). Both directions were tested for the relationships between $\delta^{15}N$ or pH and the relative abundance of functional groups or bacteria:fungi (B:F) ratio and those that improved model fit were kept. (reproduced from Fig.2 in **Paper II**; Bahram et al. 2020, with permission of the publisher)

## 4.3 The effect of colonization by root-associated fungi on tree root and soil microbiomes across Europe

To further build on the ideas presented in **Paper I** and the results presented in **Paper II**, in **Paper III** I sought to examine the effects of root colonization by EcM, AM, and DSE fungi on soil and root microbiomes across wide-ranging environmental conditions by utilizing widespread tree species across a European latitudinal gradient.

The study reported in **Paper III** found scant evidence supporting the influence of AM and EcM colonization on the structure and potential function of root and soil microbiomes, whereas root colonization by DSE fungi had a consistent effect (Figure 5). The study confirmed previous findings that EcM colonization is sensitive to moisture availability (Soudzilovskaia et al. 2015; Kennedy & Peay, 2007; Kilpeläinen et al. 2017), as indicated by the negative correlation between soil moisture and EcM colonization, and that AM colonization increases with soil pH and available host trees, which is line with AM fungi being sensitive to these factors (Bahram et al. 2020; Davison et al. 2021). It also showed that DSE colonization is highly correlated with soil C:N, consistent with DSE as indicators of harsh environments (Pandey, 2019). DSE colonization had a negative effect on the relative abundance of putative plant pathogenic fungi in soil and roots, the ratio of bacterial to fungal abundance, and bacterial diversity in soil. It also explained significant variation in the composition of fungal functional genes and N cycling genes in soil, as well as CAZyme genes, P cycling genes, and total bacterial functional genes in roots (Figure 5).

These results are consistent with the growing body of evidence that DSE associations have a suppressive effect on plant pathogens (Khastini et al. 2012; Berthelot et al. 2019; Yakti et al. 2019; Harsonowati et al. 2020; Santos et al. 2021), which may be due to physical protection of plant roots and direct antagonism against pathogens by the secretion of secondary metablites by DSE (Mandyam & Jumpponen, 2005; Terhonen et al. 2016; Berthelot et al. 2019; Santos et al. 2021). The potential for DSE to alter local abiotic conditions, such as pH (Xu et al. 2020) and the quality of soil organic matter (Mrnka et al. 2020), to which bacteria are sensitive (Rousk et al. 2010; Kuramae et al. 2012; Waring et al. 2013), may also be related to the observed effect of DSE on bacterial communities and their functional genes. Furthermore, DSE colonization was positively associated with fungal diversity in roots and total fungal functional and CAZyme gene diversity in soil, indicating DSE fungi may mediate interactions between different fungal guilds due to their unique ability to associate closely with plants yet retain free-living saprotrophic capabilities (Ruotsalainen et al.

2021), meaning they are not subject to the same obligatory constraints as mycorrhizal fungi, which require host C, or free-living saprotrophs, which lack the benefit of associating with hosts. This mediation could be enhanced in harsh environmental conditions to which DSE are better adapted (Berthelot et al. 2019; Akhtar et al. 2022).

Despite the importance of EcM and AM associations in driving a diverse array of ecological properties and processes (Read, 1991; Bennett et al. 2017; Averill et al. 2019; Steidinger et al. 2019), I demonstrate in this study that, across Europe under widespread broadleaf trees, DSE colonization has a stronger and more consistent association to soil and root microbiomes and their potential functioning than EcM and AM colonization. This suggests that in addition to mycorrhizal fungi, other root-associated fungi are likely to play a significant role in the functioning of plant-soil systems by influencing the soil microbiome, therefore there is a research need to further study the role of fungi such as DSE in mycorrhizal systems and the functioning of soil microbial communities.

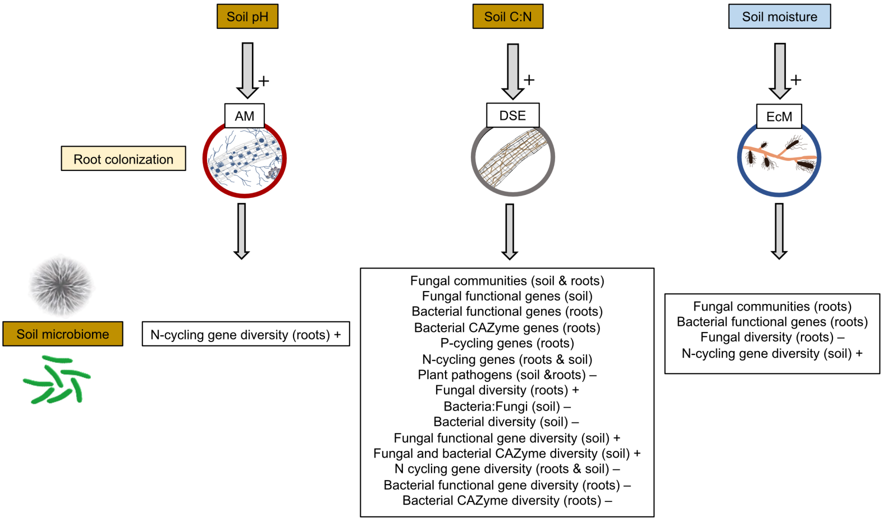

Figure 5. Conceptual figure of the main results presented in **paper III**, showing the major factors influencing root colonization rates of AM, DSE, and EcM fungi across a European latitudinal gradient, followed by the soil microbiome properties that were significantly associated with root colonization by AM, DSE, and EcM fungi. Positive correlations are denoted by ‘+’, and negative correlations by ‘–’.

## 4.4 Tree species with different root symbioses shape leaf elemental chemistry and associated microbiomes

In comparison to **Paper III**, which investigated the influence of root colonization by EcM, AM, and DSE fungi on soil and root microbiomes under widespread tree species across a European latitudinal gradient, utilizing the same trees, **Paper IV** investigated the leaf element profiles and the structure of leaf-associated bacterial and fungal communities of these tree species (Figure 6). In **Paper IV**, I sought to unravel the relative importance of host tree identity, the extent of root colonization by EcM, AM, and/or DSE fungi, surrounding vegetation, soil properties, and climate in explaining leaf element profiles and leaf-associated microbial communities, i.e., to see if leaf element profiles and microbiomes contain signatures of belowground symbiotic interactions across vastly different environmental conditions.

Firstly, I found that tree species identity, and within tree species root-symbiont colonization were important for explaining leaf elemental chemistry, along with soil properties and the proportion of EcM:AM trees and coniferous EcM trees in the surrounding vegetation. Accordingly, tree species-specific leaf elemental properties showed different patterns across latitudes (Figure 6). Leaf traits reflect a spectrum of slow, conservative, to fast, acquisitive mechanisms of resource use and investment (Reich, 2014; Díaz et al. 2016) and can reflect different types of root symbioses (Averill et al. 2019). Nevertheless, plant phylogeny and geography may confound the role of mycorrhizal type and N fixation in explaining leaf traits (Lin et al. 2017; Jantzen et al. 2023).

By focusing on widespread tree species, including three from the same family (Betulaceae), and by measuring root colonization by root-symbiotic fungi and leaf $\delta^{15}N$ to account for N fixation, I showed that leaves of N fixers (*Alnus*) had tight coupling in leaf N-related properties that distinguished them from the other species, i.e., higher N concentrations, and no distinct latitudinal trends due to their obligate symbiosis with $N_2$-fixing *Frankia* bacteria (Menge et al. 2014). Dual-mycorrhizal *Alnus* species showed little sign of P limitation across latitude, possibly due to the improved P acquisition ability of *Alnus*-associated EcM fungal communities (Walker et al. 2014) and the synergistic effect of *Frankia* and AM fungi in N and P acquisition (Oliveira et al. 2005). I also found that EcM colonization, the basal area of EcM:AM trees, and coniferous EcM trees in the surrounding vegetation explained significant variation in leaf element profiles across *Alnus* species and *Betula pendula*, but DSE colonization was also important on *A. glutinosa*, hinting at the effect of

DSE on soil microbiomes shown in **Paper III**. In comparison, on *Sorbus aucuparia*, an AM-forming species, latitude and soil properties were more important than root symbioses in explaining leaf element properties. These results highlight the complex nature of root symbioses beyond mycorrhizal types and N-fixing status, they also indicate functional variation within symbiosis types (Chaudhary et al. 2022) and flexibility in plant-nutrient acquisition strategies (Lambers et al. 2008).

Next, I examined leaf-associated bacterial and fungal communities and found that climate explained less variance in the leaf microbiome than vegetation (tree species and surrounding vegetation) and leaf element properties, especially for bacteria (Figure 6). Within tree species, bacteria and fungi on *S. aucuparia* and fungi on *A. incana* and *B. pendula* were influenced more by climate and geography than leaf elemental chemistry. For bacteria on *A. incana*, and bacteria and fungi on *A. glutinosa*, leaf element concentrations, particularly leaf Ca, were most important for explaining variance in community structure. Tree species largely determined the relative abundance of putative plant pathogenic fungi; fungal endophytes positively correlated with MAT; and both tree species and leaf Ca concentrations explained fungal alpha diversity. Leaf Ca also explained bacterial and fungal phyla and class relative abundances across species.

Host identity greatly influences leaf microbiome structure at local and regional scales (Sapkota et al. 2015; Laforest-Lapointe et al. 2016; Lajoie et al. 2020) and suggests that hosts filter leaf microbial communities (Leveau, 2019). Large-scale examinations of a single tree species (Redford et al., 2010) or multiple species from the same genus (Finkel et al., 2011) have yielded contradictory results regarding the effect of host versus climatic region. My findings in Paper IV contribute novel evidence to the field of leaf microbial biogeography by utilizing cooccurring widespread tree species and by analyzing leaf elemental chemistry to demonstrate that host identity and their leaf element profiles are generally more important than geography and climate in explaining microbiome structure (Figure 6). However, within species the effects of climate and leaf elemental chemistry are context-dependent and partially, yet indirectly, due to differences in nutrient-acquisition strategies via root symbioses. Previous research has demonstrated the importance of plant functional traits in structuring the leaf microbiome (Kembel et al., 2014; Leveau, 2019; Li et al., 2022), but this is the first study to investigate the potential effect of root symbioses (root colonization and the EcM:AM tree basal area) on leaf microbiomes by influencing leaf nutrition across multiple species and climatic biomes.

In **Paper IV**, I also highlight the importance of Ca in plant-soil systems by showing distinct patterns in leaf Ca concentrations in tree species with contrasting root symbioses across latitudes and, in turn, the potential effect this has on leaf microbiomes, which impact host performance by modulating the equilibrium between leaf health and dysbiosis (Vorholt, 2012; Vayssier-Taussat et al. 2014). Overall, **Paper IV** brings an important above-and-belowground connection to my thesis (Figure 6) and contributes additional evidence on the importance of root symbioses in shaping microbial communities in plant-soil systems, as was shown for belowground microbiomes in **Papers I–III**.

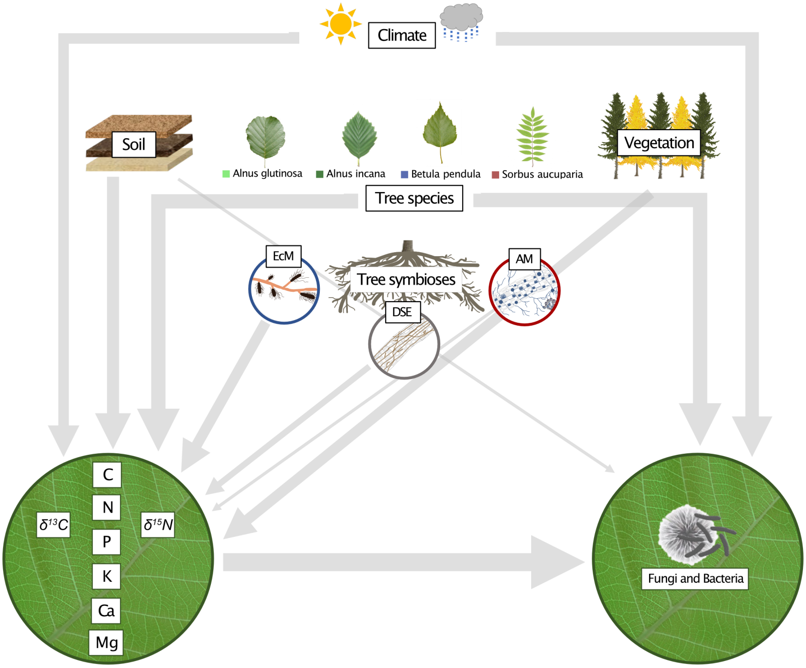

Figure 6. Conceptual figure of the study setup and main findings presented in **paper IV**; showing the major relationships explaining leaf element profiles and leaf microbiomes across Europe. The direction of the relationships is indicated by the direction of arrows, and the relative importance of relationships is indicated by the width of arrows. Tree symbioses of AM, DSE, and EcM were represented by root colonization rates and tree species, i.e., *Alnus* also forms N-fixing associations, yet N-fixing symbiosis were not directly measured, yet inferred through leaf $\delta^{15}N$ signatures.

# 5. Conclusion and future perspectives

In this thesis, I have addressed the role of plants—primarily trees—and their root symbioses in shaping soil, root, and leaf microbiomes, as well as leaf element properties, in a unique, large-scale, and broad-reaching investigation. This role has been evaluated using a variety of methods, perspectives, and scales, ranging from the effect of plant mycorrhizal type on soil microbiome structure and function in vegetation communities at the regional scale to the effect of colonization rates by root-associated fungi (EcM, AM, and DSE) on soil and root microbiomes of common tree species across a European latitudinal gradient. Furthermore, across the same tree species and gradient, I examined how host identity can explain leaf element and microbiome profiles in part through nutrient-acquisition strategies via root symbioses.

My findings on the vegetation community level demonstrate some clear differences in belowground microbial communities between AM and EcM systems. My findings at the tree level across Europe revealed inconclusive effects of EcM and AM colonization as primary predictors of microbial community properties, while a potentially strong role for DSE colonization was evident. And finally, my findings on the tree leaf level reveal that tree species and differences in their leaf element properties together largely explain leaf-associated microbial communities, and these differences may be due to different root symbioses and the surrounding vegetation.

All my studies were field-based investigations with single time point sampling and DNA-based measurements of potentially active microbial communities and their functions. While they generated many hypotheses, the actual functional implications will need to be investigated in future empirical and experimental studies that employ a broader range of *omics* techniques and direct functional measurements across temporal and spatial scales. Furthermore, while mycorrhizal types are broadly classified as AM and EcM, I have realized that it is important to acknowledge that there are other types that should be studied in the future, as well as other root-associated fungi with cryptic lifestyles. More attention should be paid to the functional variation of fungi within the symbiotic guilds of EcM, AM, and root endophytes. Furthermore, studies must include a broader range of tree species with a wider variety of traits from a range of climatic biomes to account for the geographical and phylogenetic stratification of mycorrhizal types. Common garden experiments, which can account for differences in soil conditions, still hold a lot of promise in this regard.

Lastly, soil sampling in my studies was limited to the top 5 or 10 cm of soil and cannot be generalized to deeper soil layers. Despite these limitations, my thesis contributes novel findings on soil microbiome differences between AM and EcM systems, the potentially important role of DSE fungi in structuring the soil microbiome, and the central role of tree species and the partial role of their root symbioses and leaf elemental chemistry in shaping leaf microbiomes across Europe. Overall, the results of my research indicate that biotic interactions between plants and their root symbionts are important factors in determining the structure and function of microbiomes across plant-soil systems. This suggests that under environmental change, alterations in the interactions mediated by root-symbiotic fungi between plants and soil microbiomes will determine the direction of change in plant and ecosystem functions.

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# Popular science summary

Vegetation communities, including forests formed by trees and other plants, are responsible for maintaining an astonishing array of life on Earth, including people. Nevertheless, the bacteria and fungi that live in and on plants and in the soil are crucial to their functioning. Some of these microorganisms, known as pathogens, are harmful to plants, while others, known as saprotrophs, recycle nutrients from dead plants and other organisms so that they can be used by living plants. Furthermore, others can extract nitrogen from the air, a crucial element for plant growth and development, and make it available to plants. Nevertheless, mycorrhizal symbioses with fungi constitute some of the most significant and pervasive relationships most plants form. These fungi grow in and on the roots, foraging and acquiring nutrients from the soil to exchange them with the plant for carbon, forming a mutually beneficial relationship. There are different types of mycorrhizal relationships, including those formed with ectomycorrhizal fungi or arbuscular mycorrhizal fungi, that vary in their characteristics and functions depending on the species of fungi and plants involved.

In general, plants and their mycorrhizal fungal partners may employ either a slow and conservative or a quick and acquisitive approach to nutrient cycling, which is dependent on interactions with microbial communities in the soil and on plants, including on roots. It is not well understood how exactly the broader microbial communities differ between different mycorrhizal systems depending on the traits of the plants and fungi involved and, furthermore, how this is influenced by different environments such as climates, soil conditions, and the surrounding vegetation communities. Understanding how terrestrial ecosystems and their functioning may be affected by environmental change like global warming and shifting rainfall patterns will require unravelling of the complex relationships between plants, mycorrhizal fungi, and broader microbial communities.

In this thesis, I examine how plants, different types of mycorrhizal fungi, and other root symbioses affect the structure and possible function of microbial communities in the soil and on plants, as well as the nutrient properties of leaves. I used different methods, like sequencing the DNA of microorganisms and their genes that are involved in different functions from field studies at different scales, ranging from vegetation communities in a single region to tree species that grow all over Europe.

I found that vegetation communities dominated by plants with arbuscular mycorrhizal relationships had more bacteria, fungal saprotrophs, and pathogens in their soils than sites dominated by plants with ectomycorrhizal relationships, and that coniferous ectomycorrhizal vegetation, such as spruce and pine forests, was a very important factor in determining soil conditions and the characteristics of microbial communities. Across Europe, underneath widespread deciduous tree species, I found that, compared to ectomycorrhizal and arbuscular mycorrhizal root colonization, root colonization by a different type of fungi, called dark septate endophytes, had a stronger effect on the composition of root and soil microbial communities and their genes involved in carbon and nutrient cycling and a negative effect on the proportion of fungal pathogens and bacteria. Lastly, I found that tree species with a variety of root symbioses, including nitrogen-fixing bacteria and mycorrhizal fungi, had different concentrations of leaf elements, and that this was partly related to the extent of root colonization by root symbiotic fungi. Furthermore, tree species and their leaf elements were a key factor in shaping leaf microbial communities and their diversity compared to climate across Europe.

Overall, my results suggest that in order to understand how terrestrial ecosystems and their functioning may be affected by environmental changes, we need further studies of the interactions of plants with different traits, a wide variety of root symbioses such as mycorrhizal and nitrogen-fixing symbioses, other fungi that grow in roots such as dark septate endophytes, and the multitude of other microorganisms living in the soil and on plants.

# Populärvetenskaplig sammanfattning

Växtsamhällen, inklusive skogar där det finns såväl träd som andra växter, upprätthåller en häpnadsväckande mängd liv på jorden, inklusive människor. Samtidigt är de bakterier och svampar som lever i och på växter och i jorden avgörande för hur de fungerar. Vissa av dessa mikroorganismer, kända som patogener, är växtskadegörare, medan andra, kända som saprotrofer eller nedbrytare, återvinner näringsämnen från döda växter och andra organismer så att de kan återanvändas av levande växter. Somliga mikroorganismer kan fixera kväve ur luften och leverera det till levande växter som behöver det för sin tillväxt och fortplantning. Trots detta är det emellertid med mykorrhizasvampar som växter formar de kanske mest betydelsefulla och genomgripande symbioserna. Dessa svampar växer i och på växternas rötter, genom vilka de byter näringsämnen de hämtar från jorden i utbyte mot kolföreningar i ett ömsesidigt fördelaktigt förhållande. Det finns olika typer av mykorrhizasymbioser, bland annat de som bildas med ektomykorrhizasvampar (EcM) eller med arbuskulära mykorrhizasvampar (AMF), och dessa varierar i sina egenskaper och funktioner beroende på vilka arter av svampar och växter som är involverade.

I allmänhet kan växter och deras mykorrhizasvamppartner klassificeras i relation till sin näringsomsättning som antingen långsamma och konservativa eller som snabba och förvärvande. Denna klassificering är beroende av interaktioner (samspel) med mikrobiella samhällen i jorden och på växter, inklusive på rötterna. Vi vet fortfarande lite om hur dessa bredare mikrobsamhällen i marken skiljer sig åt mellan olika mykorrhizasystem och till vilken grad olika faktorer som växtegenskaper och funktionella svampegenskaper spelar in i detta, samt hur detta i sin tur påverkas av omgivande miljöfaktorer som klimat, markförhållanden och omgivande vegetationssamhällen. För att bättre kunna förstå hur terrestra ekosystem och deras funktioner påverkas av miljöförändringar, global uppvärmning och skiftande nederbörd, krävs att vi också klargör de komplexa relationer som präglar växter, mykorrhizasvampar och de bredare mikrobsamhällena i naturen.

I denna avhandling undersöker jag hur växter, olika typer av mykorrhizasvampar och andra rotsymbioser påverkar strukturen och potentiella funktioner hos mark- och växtmikrobsamhällen, samt lövens näringsinnehåll och mikrobpåväxt. Jag har använt mig av olika metoder, som att sekvensera DNA från mikroorganismer och deras funktionella gener genom fältstudier på olika skalor, från olika biotoper i en region till trädarter som växer över hela Europa.

Mina resultat visar att i växtsamhällen som domineras av växter med arbuskulära mykorrhizasymbioser fanns det fler bakterier, svampsaprotrofer och patogener i marken jämfört med platser dominerade av ektomykorrhizavegetation. Jag fann också att en ektomykorrhizadominerad barrträdsvegetation, såsom gran- och tallskogar, påverkade både markförhållanden och mikrobsamhällenas egenskaper. När jag studerade tre lövträds-arter med utbredning över hela Europa kunde jag visa att en tredje sorts rotkoloniserande svamp som kallas för mörka septatendofyter, hade större effekt på sammansättningen av mikrobsamhällena på växtrötter och i marken, och deras funktionella gener relaterade till kol- och näringsämneskretslopp, än vad såväl ekto- som arbuskulär mykorrhizakolonisering hade. Dessutom hade mörka septatendofyter också en negativ inverkan på mängden svamppatogener och bakterier. Slutligen fann jag att trädarter som karakteriseras av symbioser med flera olika mikrober, som t.ex. kvävefixerande bakterier och mykorrhizasvampar, hade andra koncentrationer av näringsämnen i löven, jämfört med de med enbart EcM eller AMF-mykorrhiza. Detta delvis kunde förklaras av mängden rotkoloniserande symbiotiska svampar. Dessutom var trädarter och deras innehåll av näringsämnen i bladen en nyckelfaktor för bladmikrobsamhällens sammansättning och mångfald, med större effekt än klimatfaktorer över hela Europa.

Sammantaget tyder mina resultat på att för att förstå hur terrestra ekosystem och deras funktioner kan påverkas av miljöförändringar, så behöver vi fler studier av bland annat interaktioner mellan växter med olika egenskaper, en mängd olika rotsymbioser såsom mykorrhiza- och kvävefixerande symbioser och andra rotlevande svampar som mörka septatendofyter, samt myllret av alla andra mikroorganismer som lever i marken och på växter.

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# Biotic interactions with mycorrhizal systems as extended nutrient acquisition strategies shaping forest soil communities and functions

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## Abstract

Plant nutrient acquisition strategies involving ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM) associations, are key plant functional traits leading to distinct carbon (C) and nutrient dynamics in forests. Yet, little is known about how these strategies influence the structure and functioning of soil communities, and if such mycorrhizal effects may be more or less pronounced depending on the type of forest and various abiotic factors. Here we explore the potential interactions occurring between plant-EcM and plant-AM systems with the diverse soil organisms occurring in forest soils, and in the process draw attention to major issues that are worthy for future research directions. Based on these potential interactions, we suggest that EcM systems, especially those involving gymnosperms in colder climates, may select for a soil community with a narrow set of functions. These EcM systems may exhibit low functional redundancy, dominated by symbiotic interactions, where EcM fungi maintain low pH and high C/N conditions in order to tightly control nutrient cycling and maintain the dominance of EcM trees. By contrast, AM systems, particularly those involving deciduous angiosperm trees in mild and warmer climates, may facilitate a functionally more diverse and redundant soil community tending towards the dominance of competitive and antagonistic interactions, but also with a range of symbiotic interactions that together maintain diverse plant communities. We propose that the contrasting belowground interactions in AM and EcM systems act as extended nutrient acquisition traits that contribute greatly to the prevailing nutrient and C dynamics occurring in these systems.

***Keywords:*** Arbuscular mycorrhizal (AM) fungi; Ectomycorrhizal (EcM) fungi; Mycorrhizal associations; Plant-microbial feedbacks; Microbiome; Soil ecology; Holobiont; Rhizosphere; Biotic interactions

## Introduction

Soil organisms play key roles in the population and community dynamics of plants and associated carbon (C) and nutrient dynamics in terrestrial ecosystems, by acting as decomposers of soil organic matter (SOM), nutrient transformers, plant mutualists, parasites/pathogens, grazers, and predators influencing patterns of plant diversity and productivity (Baldrian, 2017; Bever, Mangan, and Alexander, 2015; Tedersoo, Bahram, and Zobel, 2020). On a global scale communities of soil organisms are mainly shaped by

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abiotic factors, such as climatic conditions and soil properties (Bahram et al., 2018; Oliverio et al., 2020; Phillips et al., 2019; Van Den Hoogen et al., 2019). On a more local scale, however, plant identity and plant functional attributes may strongly influence the community and functioning of soil organisms through direct and indirect interactions, especially those associated closely with the rhizosphere, but also those inhabiting the bulk soil (Berg and Smalla, 2009; Prober et al., 2015; Urbanová, Šnajdr, and Baldrian, 2015). Thus, plants and interacting soil organisms may essentially act as an extended holobiont (Gilbert, Sapp, and Tauber, 2012).

The strongest and most integrated interaction of the plant-soil continuum is the association between plants and mycorrhizal fungi, a root symbiosis based on C and nutrient exchange (Smith and Read, 2010). Multiple lines of evidence suggest that mycorrhizal type, in particular ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM) associations, is a key determinant of prevailing patterns of forest population and community dynamics, facilitating either co-occurrence or monodominance of tree species due to plant-mycorrhizal-soil feedbacks (Connell and Lowman, 1989; Peh, Lewis, and Lloyd, 2011). As both AM and EcM fungi associate with trees of different functional types and exist in boreal, temperate, and tropical forests, where they show contrasting dominance patterns (Öpik et al., 2010; Read, 1991; Read and Perez-Moreno, 2003; Soudzilovskaia et al., 2019), forest systems present a unique opportunity to explore contrasting ecosystem-plant-soil feedbacks.

Plant-EcM and plant-AM systems show great differences in their morphological, physiological, ecological, and phylogenetic properties (Table 1), and they are typically associated with low and high nutrient conditions, respectively, with contrasting nutrient acquisition strategies. This has led to the idea of the mycorrhizal-associated nutrient economy (MANE) (Phillips, Brzostek, and Midgley, 2013). Within this framework, AM- and EcM-dominated systems have distinct C, nitrogen (N) and phosphorus (P) cycling dynamics. AM systems tend to have high-quality litter that is rapidly decomposed by saprotrophs leading to high C mineralization, organic to inorganic N transformations, and nitrification (Phillips et al., 2013). Hence AM systems represent an inorganic nutrient economy, where AM fungi scavenge for inorganic nutrients released from litter and SOM by other soil organisms. By contrast, EcM systems tend to have low-quality litter with slow decomposition rates and most nutrients existing in organic form (Table 1). Supported by large C inputs from the host trees, EcM fungi are able to mine for organic N and P due to greater enzymatic capabilities compared to AM fungi, making less mineral N available for nitrification and losses via leaching, leading to a prevailing organic nutrient economy (Cheeke et al., 2017; Phillips et al., 2013).

However, the MANE framework is mainly based on temperate and boreal forests, and may or may not hold for tropical forests or even in temperate and boreal forests after accounting for different tree traits such as leaf habit (Averill, Bhatnagar, Dietze, Pearse, and Kivlin, 2019; Keller and Phillips, 2019; Lin, McCormack, Ma, and Guo, 2017). Furthermore, the biotic interactions occurring in soil that drive differences in nutrient and C cycling in EcM and AM systems are poorly characterised, and as most soil organisms are usually studied in isolation, we lack an understanding about the system-wide effects of trophic and ecological interactions on ecosystem functioning (Buchkowski, Bradford, Grandy, Schmitz, and Wieder, 2017; Phillips et al., 2013; Wall et al., 2008). EcM and AM systems, in combination with certain biotic and abiotic factors, may select for different soil communities and form holobionts with distinct functional properties. They are thus forming systems that exhibit *extended nutrient-acquisition strategies*, which have large implications for broad-scale C and nutrient dynamics. We propose that particular combinations of climates, trees, and mycorrhizal types influence soil community structures and ecosystem functions in contrasting ways. We also propose that EcM systems, primarily in temperate and boreal ecosystems, along with more closed nutrient cycles have a stronger and more direct influence on soil communities, leading to less functional redundancy by promoting more specialized soil organisms with a narrow set of functions that maintain a low nutrient status and slow nutrient cycling, compared to AM systems with more open and rapid nutrient cycles, and with high functional diversity and redundancy. We come to these hypotheses through exploring the interactions of EcM and AM fungi with different soil organisms in forests while considering that climatic biome and tree functional differences may strengthen or weaken specific ‘mycorrhizal effects’ on C and nutrient dynamics often associated with EcM and AM systems. We will subsequently discuss how these systems may be altered under environmental change and provide suggestions for future research needs.

**Table 1.** Overview of morphological, physiological, ecological, and phylogenetic properties of EcM and AM systems, for many properties using evidence mostly obtained from boreal and temperate ecosystems, with a clear need to investigate many of these properties in tropical ecosystems.

| **Property** | **Ectomycorrhizal fungi(EcM)** | **Arbuscular mycorrhizal fungi (AM)** |
|---|---|---|
| ***Fungal taxa involved*** (Kivlin, Hawkes, and Treseder, 2011; Öpik et al., 2013; Brundrett and Tedersoo, 2018) | Around 20,000 different fungal taxa, mainly from the phylum Basidiomycota, but also Ascomycota and Zygomycota | 250–1000 fungal taxa from the phylum Glomeromycota |
| ***Plant taxa involved*** (Brundrett and Tedersoo, 2018;) | 2% of terrestrial plants, mainly woody | 72% of terrestrial plants across a broad phylogeny |
| ***Specialized structures in and on host roots*** (Bonfante and Genre, 2010) | Intercellular hartig net and hyphal mantle ensheathing the root tip representing high fungal to root biomass. | Highly branched intracellular arbuscules representing less fungal to root biomass compared to a mantle and hartig net |
| ***External mycelium*** (Agerer, 2001; Chagnon et al., 2013 | Extensive and varied with contrasting functional exploration types | Less extensive and more homogenous types |
| ***Reproductive and dispersal strategies*** (Horton, 2017; Vašutová et al., 2019) | Sexual or asexual reproduction, often production of fruiting bodies that facilitate wind and animal dispersal | Asexual reproduction, production of large asexual resting spores, relying on active and passive animal dispersal |
| ***Provision of C from host plants*** (Tedersoo and Bahram, 2019) | 7–30% of photosynthates | 2–20% of photosynthates |
| ***Hyphal turnover*** (Finlay and Read, 1986; Staddon, Ramsey, Ostle, Ineson, and Fitter, 2003; Olsson and Johnson, 2005; Wallander, 2006; Ekblad et al., 2013; Pepe, Giovannetti, and Sbrana, 2018) | 2 weeks to 7 months, or even up to 2–10 years | 4–5 days, to weeks and potentially months |
| ***Provision of nutrients to host plants*** (Smith, Smith, and Jakobsen, 2003; Smith and Smith, 2012; Phillips et al., 2013; Tedersoo and Bahram, 2019) | Organic and inorganic N acquisition is most important, but can also access inorganic P perhaps more efficiently than AM fungi | Inorganic P acquisition most important, and can acquire both inorganic and organic N, but may compete with host plants for N |
| ***Enzymatic capacity to break down organic matter*** (Tedersoo and Bahram, 2019) | Low to high enzymatic capacity for organic nutrient acquisition depending on EcM species/lineages, although less capacity compared to saprotrophic fungi | Lacking |
| ***Litter quality of hosts and decomposition*** (Read, 1991; Tedersoo and Bahram, 2019) | Low-quality, slower decomposition | High-quality, faster decomposition |
| ***Factors driving root colonization intensity, external mycelium production*** (Nilsson, Giesler, Bååth, and Wallander, 2005; Soudzilovskaia et al., 2015; Wang, Zong, and Li, 2019) | Colonization highest in acidic soils and mesic climates with constant precipitation. Mycelium production negatively correlated with nutrient availability | Colonization highest under continental climates with mild summers and high soil N availability. Mycelium production positively correlated with nutrient availability. |
| ***Proposed prevailing nutrient economy*** (Phillips et al., 2013; Averill et al., 2019; Tedersoo and Bahram, 2019) | Conservative closed organic nutrient economy | Rapid open/leaky inorganic nutrient economy |
| ***Relationship to top-soil C stocks*** (Soudzilovskaia et al., 2019) | EcM basal area fraction positively correlated with top-soil C stocks | AM basal area fraction negatively correlated with top-soil C stocks |
| ***Contribution to tree basal area across forest biomes*** (Steidinger et al., 2019) | >90% of boreal forest basal area, around 75% of temperate forest basal area, and < 30% of tropical forest basal area | 60–70% of tropical forest basal area, > 20% of temperate forest basal area, and < 5% of boreal forest basal area |
| ***Plant-soil feedbacks*** (Bennett et al., 2017) | Neutral to positive | Negative |

## BOX 1. Tree and mycorrhizal types as key plant nutrient-acquisition traits across forest biomes

**The EcM symbiosis requires a greater investment of C from the host plant than the AM symbiosis, equating to a more obligatory relationship with less autonomy for the host, a physical barrier between its roots and the soil environment, and a greater extension of its zone of influence in the soil (Table 1).Thus, EcM systems represent a more closed, stable and specialized active nutrient acquisition strategy that is less reliant on other soil organisms for nutrient transformation and more competitive against these organisms and AM trees under limiting nutrient conditions (Phillips et al., 2013; Cheeke et al., 2017; Averill et al., 2019). However, EcM systems are perhaps more vulnerable to disturbance and environmental change due to less flexibility for the plant in the symbiosis, requiring more stable mesic conditions for success (Table 1). On the other hand, the AM symbiosis gives the plant more autonomy in the soil with greater root-soil contact (Tedersoo and Bahram, 2019), they have a greater reliance on other soil organisms for nutrient transformations (Phillips et al., 2013), a greater competitive ability compared to EcM trees under high nutrient conditions, and a greater safety net for the plant against disturbance and environmental change due to a greater flexibility for the plant in the symbiosis (Table 1).**

**In addition to mycorrhizal types, trees can be angiosperms or gymnosperms, further divided into deciduous or evergreen, which differ in their distributions and commonality. Angiosperms tend to outcompete gymnosperms and become dominant in most tropical and temperate forests, while gymnosperms tend to dominate in cold and/or nutrient-poor soils, representing fast versus slow plant economic traits (Bond, 1989; Reich, 2014). Accordingly, gymnosperms have greater longevity of their organs (foliage, stems and roots), facilitated by the production of resins rendering protection from fungal and insect attack, whereas angiosperms tend to be more susceptible to such attacks (Brodribb et al., 2012). The deciduous habit is more common in angiosperms compared to gymnosperms for whom the evergreen habit is more common (Gower and Richards, 1990; Reich et al., 1997). And the greatest functional difference in fast versus slow plant economic traits in trees occurs between evergreen gymnosperms and deciduous angiosperms, with slower growth rates, conservative nutrient cycling, lower decomposition rates, and thicker litter layers under the former (Augusto et al., 2015; Dawud et al., 2017; Angst et al., 2019).**

**Different tree and mycorrhizal types also exist across forest biomes that have varying aboveground biomass C stocks, soil C stocks, nutrient dynamics and climatic conditions (Read, 1991). Despite large climatic differences, tropical forests are usually more biomass C dense and contribute more to global forest aboveground biomass than temperate and boreal forests (Crowther et al., 2015; Liu et al., 2015). While boreal forests contribute around a half to total global forest soil C stocks despite only covering a third of the global forest area, tropical forests, despite accounting for over half of global forest area, contribute only around a third of global soil C (Scharlemann et al., 2014; Keenan et al., 2015). In addition, boreal forests have a belowground C flux of around two thirds of their gross primary production, compared to around a half in temperate forests, and around a third in tropical forests (Gill and Finzi, 2016). Tropical forests tend to have rapid nutrient cycles and produce high-quality litter compared to boreal forests that have slow nutrient cycles and low-quality litter, with temperate forests in between (Vitousek, 1982). Nitrogen becomes increasingly limiting from tropical to boreal forests, while phosphorus is more limiting in tropical forests, accordingly, although there is heterogeneity in nutrient limitations within biomes (Vitousek et al., 2010; Gill and Finzi, 2016).**

**These broad scale observations on C and nutrient dynamics across biomes warrant further attention for differences in tree functional traits including mycorrhizal type, given that boreal forests are dominated by gymnosperms, while temperate and tropical forests are dominated by angiosperms (Poulter et al., 2011; Augusto et al., 2015; Crowther et al., 2015). Boreal gymnosperm forests potentially have around a two-fold higher soil C density, while in temperate and tropical forests soil C content appears to be more equal between gymnosperms and angiosperms (Zhong and Qiguo, 2001; Vesterdal et al., 2013). Furthermore, around 60% of the worlds standing trees may be EcM-forming, distributed mostly across boreal and temperate forests, while AM-forming trees make up most of the remaining 40% concentrated mostly in the tropics (Steidinger et al., 2019). Soil C is positively related to the abundance of EcM trees but differs depending on biome (Soudzilovskaia et al., 2019). The different leaf habits are also unequally distributed across biomes, deciduous trees are found mostly in temperate and tropical forests, and evergreen trees in boreal and tropical forests (Poulter et al., 2011; Crowther et al., 2015). Understanding these traits across forest biomes is important as they may strengthen or weaken the prevailing closed versus open nutrient dynamics of EcM and AM systems, which may profoundly affect soil community structures and functions.**

## Ecosystem-tree-mycorrhizal interactions with soil organisms as extended nutrient-acquisition traits

Mycorrhizal fungi interact directly and indirectly with other soil organisms, while also moderating plant interactions with these organisms. Such interactions span a spectrum from inhibition to stimulation and direct competition to mutualism (Fitter and Garbaye, 1994), and drive and maintain distinct C and nutrient dynamics (Averill et al., 2019; Cheeke et al., 2017; Phillips et al., 2013; Read, 1991). While there is some overlap between EcM and AM in their interactions with soil organisms, they likely have contrasting effects when it comes to facilitation and inhibition of these organisms. EcM fungi, especially when associating with gymnosperms in temperate and boreal forests, represent a potentially greater facilitator or inhibitor of soil biotic activity compared to AM fungi. This is because of the greater physical presence of EcM in the soil, their greater enzymatic capacity and activity (Tedersoo and Bahram, 2019), their greater tolerance and potential maintenance of acidic soil conditions (Rosling, Lindahl, Taylor, and Finlay, 2004), and their contribution to and maintenance of high C/N ratios in the soil (Franklin, Näsholm, Högberg, and Högberg, 2014; Lin et al., 2017; Tedersoo and Bahram, 2019). This has the potential to trap systems in an N-limited state (Franklin et al., 2014), as it affects factors which other soil organisms are sensitive to (Bahram et al., 2018; Fierer, 2017).

## Mycorrhizal interactions with saprotrophs

The interaction of mycorrhizal fungi with soil saprotrophs is considered to be a major factor influencing patterns of soil C and nutrient dynamics in forest soils (Averill, Turner, and Finzi, 2014; Brzostek, Dragoni, Brown, and Phillips, 2015; Fernandez and Kennedy, 2016; Sterkenburg, Clemmensen, Ekblad, Finlay, and Lindahl, 2018). These interactions are generally seen as either inhibitory or stimulatory (Fitter and Garbaye, 1994; Frey, 2019). The inhibition of soil saprotrophs, specifically saprotrophic fungi, by mycorrhizal fungi is known as the 'Gadgil effect', and refers to the phenomenon of EcM fungi suppressing the activity of fungal saprotrophs leading to decreased decomposition rates, or the removal of EcM from a system enhancing decomposition rates (Gadgil and Gadgil, 1971, 1975; Fernandez and Kennedy, 2016). This is thought to be driven primarily by the competition for organic matter colonization between EcM fungi and saprotrophic fungi. Fueled by a large input of C from host trees, some EcM fungi are able to proliferate and selectively mine for N in organic matter (Lindahl and Tunlid, 2015), in the process potentially outcompeting saprotrophic fungi and leading to C accumulation (Fernandez and Kennedy, 2016; Sterkenburg et al., 2018).

The 'Gadgil effect' has mostly been observed under temperate and boreal evergreen gymnosperm trees (Gadgil and Gadgil, 1971, 1975; Averill and Hawkes, 2016; Fernandez and Kennedy, 2016), and may not hold for deciduous angiosperm trees in the same systems (Fernandez, See, and Kennedy, 2019), nor under tropical evergreen angiosperm N-fixing trees (Mayor and Henkel, 2006). Furthermore, the presence of certain saprotrophic fungi can be higher in EcM gymnosperm forests compared to other EcM and AM forests (Awad et al., 2019; Bahram et al., 2020), although overall decomposition is still likely to be slow. While there is a lack of studies of the 'Gadgil effect' across different types of forests, it may be specific to EcM forming gymnosperms in boreal and temperate forests. Although first described in introduced *Pinus radiata* plantations in New Zealand (Gadgil and Gadgil, 1971, 1975), it may be most pronounced or at least saprotrophic activity most reduced in ecosystems with a significant ericoid mycorrhizal component (Clemmensen et al., 2015), which have an even greater saprotrophic capability than EcM fungi (Martino et al., 2018). Ericoid mycorrhizal fungi produce highly melanized mycelium that is resistant to decomposition (Clemmensen et al., 2015), and their hosts have very low-quality litter (Read, Leake, and Perez-Moreno, 2004). These factors suggest that ericoid mycorrhizal fungi and their plant symbionts may form an even more closed nutrient cycle in their zone of influence, outcompeting other fungal guilds for organic nutrient resources (Wurzburger and Hendrick, 2009). Something resembling the 'Gadgil effect' has been shown among certain tropical tree species, where the presence of mycorrhizal hyphae retarded root litter decomposition under tropical evergreen EcM gymnosperms as well as evergreen AM gymnosperms and angiosperms in the same system (Lin, Chen, and Zeng, 2019), suggesting that AM fungi may also suppress saprotrophic activity in forests, although this is not well supported.

When saprotrophs are C limited, and labile forms of C are quickly depleted, the exudation of labile C by tree roots and mycorrhizal fungi can stimulate saprotrophic breakdown of more complex C forms, for which they would otherwise be energy-limited to do so, a mechanism commonly known as 'priming' (Brzostek et al., 2015; Fernandez and Kennedy, 2016; Verbruggen, Pena, Fernandez, and Soong, 2017). Both EcM and AM fungi have been implicated in priming of decomposition (Clemmensen et al., 2015; Hodge, 2014), which is in contradiction to the 'Gadgil effect'. Even though most evidence for AM-induced priming comes from non-forest systems, AM fungi have been found to colonize both fresh and partially decayed litter in a variety of forests across biomes, as well as having higher colonization rates in upper organic soil layers (Bunn, Simpson, Bullington, Lekberg, and Janos, 2019; Sheldrake et al., 2017). From these observations it is tempting to speculate that AM fungi may engage in highly directed priming of saprotrophs via release of soluble C in nutrient-rich patches and scavenge for the mineralized nutrients released by saprotrophic activity (Bunn et al., 2019; Kaiser et al., 2015; Sheldrake et al., 2017).

However, it is relatively unknown whether decomposition of litter in AM systems is directly enhanced by the activity of AM fungi or is already rapid due to high-quality litter inputs, where AM colonization of litter may be inconsequential for overall C dynamics. In addition, plant roots may act as the main primers of soil saprotrophs and may do so in a more passive and diffuse way (Kuzyakov, Friedel, and Stahr, 2000; Shahzad et al., 2015), compared to mycorrhizal fungi (Kaiser et al., 2015). It is difficult to untangle the relative contribution of plant roots and mycorrhizal fungi to these processes (Verbruggen et al., 2017). Nevertheless, given that AM trees tend to have greater direct root-soil access compared to EcM trees, whose root-soil interactions are governed more tightly by EcM fungi, AM trees may be responsible for more priming through a combination of highly directed soluble C release by AM fungi and passive and general soluble C release by AM tree roots. This is in line with the more rapid nutrient cycling of AM systems with greater saprotrophic activity (Phillips et al., 2013), as there appears to be a greater capacity for AM systems to support a wider variety of saprotrophs, compared to EcM systems, where saprotrophic fungi that have efficient ligninolytic enzyme capabilities are more prominent (Bahram et al., 2020). In EcM systems, however, the high EcM mycelial biomass in the soil is likely a major resource for saprotrophs (Brabcová, Nováková, Davidová, and Baldrian, 2016), and has been shown to turnover rapidly (Clemmensen et al., 2015). Furthermore, EcM and fungal saprotrophs may co-exist by inhabiting different spatial niches especially in boreal forests with deep mor layers (Kyaschenko, Clemmensen, Karltun, and Lindahl, 2017).

Overall it is likely that mycorrhiza-saprotroph interactions occur on a spectrum of inhibition to stimulation and are likely to be spatially and temporally heterogenous. Thus, the so called ‘Gadgil’ and ‘priming’ effects are context-dependent and may both occur in the same system separated in space and time. In EcM systems, especially under N limitation such as boreal gymnosperm forests, regulation or suppression of decomposition is facilitated by the input of low-quality litter by EcM plants, allowing for a tighter control on C and nutrient cycling (Smith and Wan, 2019). AM systems, on the other hand, may favor stimulatory and neutral interactions with saprotrophs, relying on their activity for mineralization of organic nutrients that they scavenge for, with reduced control on C and nutrient cycling (Frey, 2019). Yet there is a lack of integration and consideration of these interactions across climatic biomes and tree types. Furthermore, most studies on mycorrhizal interactions with saprotrophs and patterns of decomposition focus on fungal saprotrophs, because fungi are considered the primary decay agents of complex plant-derived C (Baldrian, 2017). However, evidence suggests that the contribution of bacterial saprotrophs to forest soil decomposition has likely been underestimated (Lladó, López-Mondéjar, and Baldrian, 2017). Bacteria are extremely diverse and abundant in soils and have been shown to be capable of decomposing complex C substrates (López-Mondéjar et al., 2018). Compared to fungal saprotrophs who may be better suited to utilize plant compounds, bacteria may be better suited to utilize fungal and bacterial necromass (Lladó et al., 2017; López-Mondéjar et al., 2018), and may dominate in the decomposition of EcM mycelia in particular (Brabcová et al., 2016). It may well be that the activity of fungal saprotrophs promotes the activity of bacterial saprotrophs, through their substrate and decay stage niche separation (Romaní, Fischer, Mille-Lindblom, and Tranvik, 2006), further enhancing decomposition and partly explaining the contrasting C and nutrient dynamics in EcM and AM systems. Thus, the relative contributions of fungi and bacteria to decomposition in EcM and AM systems presents an important research area, as more complete decomposition of both plant and microbial biomass may require the activity of both saprotrophic bacteria and fungi (López-Mondéjar et al., 2018).

## Mycorrhizal interactions with pathogens

Plant-soil feedbacks involving plant antagonists such as pathogens have long been recognized to influence patterns of forest diversity and plant succession (Connell, 1971; Janzen, 1970; Van Der Putten, 2000). The holobiont perspective combined with the contrasting patterns of interactions between trees and EcM and AM fungi with soil-borne pathogens (fungi, bacteria, protists, viruses, and nematodes) across climatic biomes adds a new perspective that may help explain distinct and differing plant and soil community dynamics and functioning.

Accumulating evidence points to relatively greater soil-borne pathogen prevalence in AM systems compared to EcM systems, resulting in greater negative plant-soil feedbacks in the former compared to positive and neutral feedbacks in the latter (Bahram et al., 2020; Bennett et al., 2017; Chen et al., 2019; Kadowaki et al., 2018; Teste et al., 2017). It is possible that if there are increased competition and interactions between different microbial groups in AM systems, this may lead to increased functional switching from saprotrophic or commensal microbes to pathogenic microbes in those capable of such switching, as proposed under the pathobiome concept (Vayssier-Taussat et al., 2014). Pathogens may also benefit from high nutrient access or less competition with AM fungi for colonizing roots of AM hosts (Ingham, 1988), compared to greater physical protection of EcM roots by EcM fungi (Branzanti, Rocca, and Pisi, 1999). In addition, a relatively stable source of N as shown in EcM trees facilitated by organic N acquisition by EcM fungi (Corrales, Mangan, Turner, and Dalling, 2016), may promote plant defense responses if N can be consistently allocated to secondary metabolite production (Blodgett, Herms, and Bonello, 2005). This greater activity of pathogens in AM systems leads to greater negative density dependence of AM trees and potentially drives plant community and population dynamics, facilitating higher tree species richness in AM-dominated systems (Chen et al., 2019; Laliberté, Lambers, Burgess, and Wright, 2015; Tedersoo, Bahram, and Zobel, 2020). By contrast, the suppression of pathogens by EcM trees may contribute to positive and neutral plant-soil feedbacks facilitating monodominant conspecific EcM systems from the tropics to the boreal forest (Connell and Lowman, 1989; Corrales et al., 2016; Dickie, Koele, Blum, Gleason, and McGlone, 2014; Tedersoo, Bahram, and Zobel, 2020). Recent evidence suggests that the Janzen-Cornell hypothesis may have limitations in explaining plant diversity. On a broad scale, monodominant EcM systems may be an exception rather than the rule and related more to edaphic factors (Ter Steege et al., 2019). It is also possible that mixed EcM/AM forests facilitate more diverse plant communities through a combination of negative, positive, and neutral plant-soil feedbacks (Bahram et al., 2020), that would create establishment mosaics for plants with differing regeneration niches (Mariotte et al., 2018). The next step in studying mycorrhizal-pathogen dynamics is to go beyond mere relative and absolute pathogen abundance analyses in these systems to analyzing actual pathogen attack or damage to mycorrhizal hosts, perhaps by detecting and quantifying necrosis (Minina et al., 2013), and relating this to mycorrhizal root colonization and community analysis.

One additional particular topic of interest for future research is the role of viruses in mycorrhizal systems, as viruses through cell lysis may be responsible for a large fraction of C that cycles in the soil food web (Kuzyakov and

Mason-Jones, 2018) And they are also key mediators of horizontal gene transfer within and potentially across kingdoms (Kimura, Jia, Nakayama, and Asakawa, 2008). Phages play an obvious role in controlling bacterial populations, but viruses also infect all other organisms in the soil (Pratama and van Elsas, 2018). A recent study showed that viruses that infect eukaryotic hosts, mostly fungi, appear to be more diverse than phages in soils (Starr, Nuccio, Pett-Ridge, Banfield, and Firestone, 2019). Thus, viruses of eukaryotes likely play an important role in fungal community dynamics, as well as C and nutrient dynamics in EcM systems with high fungal biomass, compared to AM systems where phages may play a greater role in bacterial community dynamics, as well as C and nutrient dynamics, due to higher bacterial biomass (Kimura et al., 2008; Kuzyakov and Mason-Jones, 2018). Such questions could be addressed by combining stable isotope probing with ‘omics’ techniques to unravel if mycorrhizal systems host distinct viral assemblages with contrasting C and nutrient flows through their associated viromes, but general studies into viral communities using amplicon sequencing will also be useful in advancing this research area.

## Mycorrhizal interactions with soil grazers and predators

The contrasting food web dynamics of AM and EcM systems is driven by their contrasting dominant energy channels; where AM systems with more rapid nutrient cycling have a more bacterial-based energy channel and EcM systems with slower nutrient cycling have a more fungal-based energy channel (Phillips et al., 2013; Wardle et al., 2004). These energy channels may then merge at trophic levels due to the omnivorous feeding of many soil animals (Bengtsson, Setälä, and Zheng, 1996) or by the activity of protists who are major feeders on both bacteria and fungi (Geisen, 2016). Given their different nutrient economies, EcM and AM systems are expected to have very different food webs driven by multitrophic interactions, and hence these mycorrhizal associations influence the whole ecosystem surrounding plants including associated soil animals and protists.

The high bacterial to fungal biomass ratio of AM systems as well as less AM protection of roots should promote a higher density of bacterivores (primarily protists and nematodes) and herbivores (root-feeding invertebrates like nematodes), and their subsequent predators and pathogens (Antunes and Koyama, 2017; Persson, Bengtsson, Menge, and Power, 1996). The high fungal biomass of EcM systems should promote a higher density of fungivores (various invertebrates and protists), and their subsequent predators (Antunes and Koyama, 2017; Cromack, Fichter, Moldenke, Entry, and Ingham, 1988; Fitter and Garbaye, 1994). While little is known about the effect of mycorrhizal type on nematode community dynamics, evidence suggests that fungal-feeding nematodes have higher abundances under EcM trees, compared to bacterial-feeding nematodes under AM trees (Cesarz et al., 2013). This observation may however be ascribed to the strong pH effect on bacterial community structure (Fierer, 2017), rather than mycorrhiza *per se*. Furthermore, EcM fungi may provide more extensive and nutritious hyphae for fungivores compared to saprotrophic fungi which dominate AM forests (Anslan, Bahram, and Tedersoo, 2018; Cromack et al., 1988; Dighton, Zapata, and Ruess, 2000).

Protists may be key organisms that help to maintain higher diversity and system functioning in the soil community through consumption of bacteria and fungi, control of their populations, and release of excess N that can be utilised by other organisms (Clarholm, Bonkowski, and Griffiths, 2007; Coleman, 1994; Gao, Karlsson, Geisen, Kowalchuk, and Jousset, 2019). This N may be preferentially targeted for uptake by AM fungi, which may be an important source of N for AM hosts (Koller, Rodriguez, Robin, Scheu, and Bonkowski, 2013). We suggest that the importance of protists in N liberation is less important in EcM systems due to the tight control of EcM on N cycling, yet protists may be important in the turnover of EcM biomass, from which N can be recycled back through the EcM symbiosis, and protists may also play an important role in EcM fungal community dynamics (Gao et al., 2019; Geisen et al., 2016). But ultimately the activity of protists may be influenced by mycorrhizal mycelium which connects soil patches of nutrients and soil moisture (Jentschke, Bonkowski, Godbold, and Scheu, 1995), which protists are sensitive to and require for movement and functioning (Geisen, Bandow, Römbke, and Bonkowski, 2014). Yet, further studies into protist communities from a mycorrhizal type perspective are warranted, especially given the respective N cycling effects associated with EcM and AM systems (Phillips et al., 2013). As protists have been found to be more sensitive to N addition compared to other soil microbes in agricultural systems (Zhao et al., 2019), it remains to be investigated whether such effects of N availability on protist communities may occur in forest settings across an EcM to AM dominance gradient.

The presence of earthworms also plays an important role in C and nutrient dynamics in tree-mycorrhizal systems, by reducing soil organic layer thickness, altering bulk density, and mixing organic matter with mineral soils across soil horizons (Filser et al., 2016; Frelich et al., 2006; Van Groenigen et al., 2014). Aside from climate, the presence and activity of earthworms is driven mostly by the availability of high-quality litter (De Wandeler et al., 2018; Szlavecz et al., 2018), and impeded by low pH (Phillips et al., 2019). Earthworms can be grouped into three functionally distinct groups according to their burrowing behaviours. Burrowing anecic and endogeic worms are associated with mull formation in forest soils, whereas, in mor soils usually only epigeic (surface-living earthworms) are found (Bouché, 1977; Satchell, 1983). While not directly explored from a mycorrhizal type perspective, across temperate and boreal forests earthworm biomass, species richness and the occurrence of epigeic earthworms have been found to be lowest in forests with a greater evergreen (EcM) gymnosperm fraction and highest in forests with a greater deciduous (AM) angiosperm fraction (De Wandeler et al., 2018), largely consistent with the effects of lower pH on earthworms. Consequently, at least in certain temperate forests, the dominant feeding source of earthworms may also vary between EcM- and AM-dominated systems, with epigeic and anecic fresh litter feeders dominating in younger (AM-dominated) systems and endogeic soil organic matter feeders dominating in older (EcM-dominated) systems (Szlavecz et al., 2018). The role and distribution of earthworms in tropical forests is more complex to interpret from an EcM and AM system perspective.

## Mycorrhizal interactions with N-transforming microbes

Bacteria are the most abundant and diverse free-living organisms in soils acting as key N-fixing microbes, nitrifiers, and denitrifiers (Lladó et al., 2017; López-Mondéjar et al., 2018). Archaea are also widely distributed in soils and include members who play potentially important roles in soil N cycling as ammonia-oxidizing archaea (AOA) (Bates et al., 2011; Cavicchioli, 2011). The contrasting N dynamics of EcM and AM systems is largely owing to their interactions with microbes involved in N fixation and subsequent transformations, as mycorrhizal fungi lack the ability to fix atmospheric N or carry out nitrification.

Both EcM and AM fungi interact with N-fixing bacteria, which can provide a substantial amount of N input to these systems (Pastor and Binkley, 1998; Son, 2001). N-fixing tree symbioses occur in both EcM and AM systems but are most abundant in tropical AM systems (Steidinger et al., 2019). Yet rhizobial N-fixing trees in tropical forests tend to be insensitive to soil N availability, and more facultative in their relationship with their N-fixing symbionts (Vitousek et al., 2002), while actinorhizal temperate and boreal N-fixing trees are more sensitive to soil N availability with a more obligatory relationship with their N-fixing symbionts, which are more crucial for plant N acquisition (Menge, Lichstein, and Ángeles-Pérez, 2014; Vitousek, Menge, Reed, and Cleveland, 2013). The success of actinorhizal N-fixing trees, that grow quickly at early successional stages and are later outcompeted by non-fixing trees (Liao and Menge, 2016), is likely related to the relative proportion of EcM to AM trees. AM systems may have greater turnover of canopy trees and gap creation with heterogeneity in successional stages suitable for the establishment of shade intolerant actinorhizal N-fixing trees, compared to monodominant EcM systems (Tedersoo, Bahram, and Zobel, 2020). AM trees also likely depend more on symbiotic N fixation for their nutrient economies, due to a looser control on N dynamics and reliance on other organisms for N liberation, including a potentially higher reliance on atmospherically fixed N especially in N-limited ecosystems (Averill et al., 2019; Bagyaraj, 1990; Barea, Azcon, and Azcón-Aguilar, 1992). However, it should be noted that boreal forests dominated by EcM gymnosperms have a significant moss component, where moss-cyanobacterial associations may be responsible for a significant input of N into these systems, which can be cycled through the EcM symbiosis, however this N is potentially only released into the soil slowly or after disturbances (Carleton and Read, 1991; Rousk, Jones, and DeLuca, 2013).

The contribution of free-living N-fixing bacteria in the soil to overall N fixation tends to be smaller compared to symbiotic N fixation and is less explored across biomes and across mycorrhizal types, however, there seems to be little difference between gymnosperm and angiosperm forests in this respect (Reed, Cleveland, and Townsend, 2011; Son, 2001). This N can be a significant input into forests with few symbiotic N-fixing bacteria such as boreal and temperate forests, and in evergreen compared to deciduous forests (Reed et al., 2011). AM systems stand to benefit more from the activity of free-living N-fixing bacteria in soils. Yet, the more extensive EcM mycelium is associated with greater moisture and soluble C sources compared to the bulk soil, and may provide good habitat for free-living bacteria who require high-quality soluble C in order to undertake N fixation, although at the same time decreased pH in the ectomycorrhizosphere may inhibit N fixation (Smercina, Evans, Friesen, and Tiemann, 2019). Both EcM and AM trees host non-nodulating endophytic N-fixing bacteria, which may not only play important roles in N acquisition but also in the establishment and maintenance of the mycorrhizal symbiosis (Aghai et al., 2019; Oses, Frank, Valenzuela, and Rodríguez, 2018).

While N fixation is important for N dynamics, subsequent nitrification is dependent on the activity of both ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB), and then nitrite-oxidizing bacteria (NOB) to complete the nitrification process (Stempfhuber et al., 2017). AOA are thought to dominate in nutrient-poor and acidic soils and are outcompeted by AOB with increasing N availability (Bates et al., 2011; Di et al., 2009; Xiang, He, He, Myrold, and Chu, 2017). Thus, it is expected that AOB would dominate ammonia-oxidation in AM systems, compared to the dominance of AOA in EcM systems. Overall, nitrification tends to be lower in EcM systems compared to AM systems (Lin et al., 2017), due to enhanced competition by EcM fungi for N with nitrifying prokaryotes (Tatsumi, Taniguchi, Du, Yamanaka, and Tateno, 2019), and a potential mismatch between ammonia-oxidizing microbes and nitrite-oxidizing microbes in EcM systems, particularly under EcM gymnosperm trees, who may even inhibit the activity of AOA despite often being associated with low pH conditions (Isobe et al., 2012;

Stempfhuber et al., 2017; Stopnišek et al., 2010). It is tempting to speculate that in AM systems more so than in EcM systems, AOB and NOB may form a symbiosis enhancing the nitrification process (Daims, Lücker, and Wagner, 2016), facilitated by higher N availability and pH values (Averill et al., 2019; Lin et al., 2017; Tedersoo and Bahram, 2019). While general patterns of soil N cycling and the contribution of different organisms remain unresolved across different forest biomes, mycorrhizal and tree types, the conservative N economy of EcM systems and the open N economy of AM systems are seen as the defining contrasting functional and ecological trait between the two, as shown mainly in temperate forests (Averill et al., 2019; Lin et al., 2017; Phillips et al., 2013), and interactions with N-transforming microbes likely play a large role in these differences.

## EcM-AM interactions

Another important and often overlooked interaction is between EcM and AM fungi, because they often coexist in various ecosystems and even on the same tree individual (Kubisch, Hertel, and Leuschner, 2016; Teste, Jones, and Dickie, 2019; Toju, Sato, and Tanabe, 2014). AM systems may facilitate the establishment and survival of EcM trees, while EcM systems may impede the establishment and survival of AM trees (Kadowaki et al., 2018; Tedersoo, Bahram, and Zobel, 2020). Furthermore, the mycelium of AM and EcM fungi may co-occur in the same niche or occur via spatial separation in the soil profile (Moyersoen, Fitter, and Alexander, 1998; Teste, Jones, and Dickie, 2019). In addition, increasing evidence shows that when growing together on the same root system, AM and EcM may have a synergistic effect on plant-soil functioning, which seems to be driven by extreme environmental fluctuations such as soil moisture, nutrient availability, and temperature, where EcM may dominate colonization under mesic conditions and AM under extreme soil moisture conditions, and high temperatures and nutrient availability (Teste, Jones, and Dickie, 2019). Yet little is known about the actual physical and chemical interactions between the mycelia of EcM and AM fungi when in the vicinity of one another, with obvious difficulties in exploring this. Greater antagonisms may exist within guilds between functionally equivalent taxa as opposed to between EcM and AM fungi, due to competition for colonization sites, ultimately regulated by the host's attempt to balance C and nutrient budgets

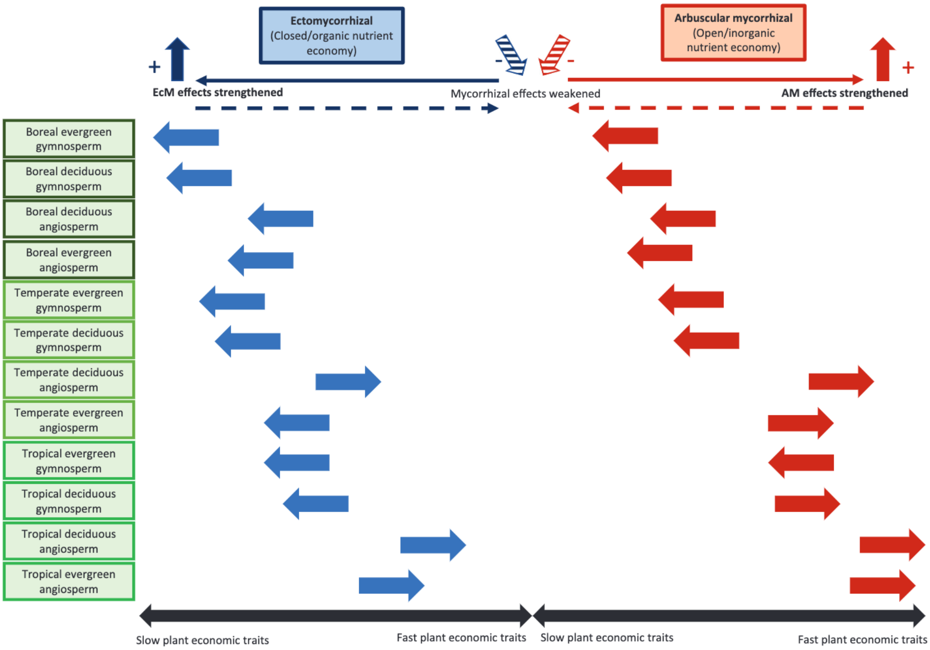

**Fig. 1.** Conceptual diagram exploring the relative trade-offs between strengthening and weakening effects on the closed and open nutrient economies of EcM and AM systems by different tree functional trait and forest biome combinations. The position and direction of arrows of the different tree/biome combinations is relative to their suggested balance between strengthening or neutralizing/weakening effects on EcM- or AM- associated nutrient dynamics and where these combinations sit on the plant economic trait spectrum.

(Bogar et al., 2019; Hortal et al., 2017; Smith and Smith, 2012).

## Mycorrhizal fungi select for distinct soil communities

Overall, the EcM symbiosis represents a trade-off between conservative nutrient acquisition and flexibility, with EcM trees tending towards collaboration in nutrient acquisition, while the AM symbiosis represents a flexible and rapid nutrient acquisition over security trade-off, with AM trees tending towards 'do it yourself' nutrient uptake but also engaging in collaboration (Averill et al., 2019: Bergmann et al., 2020). These trade-offs may be further exacerbated due to different tree types and also different climatic biomes, where the combination of EcM with gymnosperms in boreal forests represents the extreme of slow plant economic traits and the combination of AM with angiosperms in tropical forests represents the extreme of fast plant economic traits (Fig. 1) (Augusto et al., 2015; Bond, 1989; Phillips et al., 2013; Vitousek, 1982). Within biomes and tree types, the greatest difference is likely between evergreen EcM trees and deciduous AM trees (Fig. 1) (Angst et al., 2019; Augusto et al., 2015; Dawud et al., 2017; Vesterdal, Clarke, Sigurdsson, and Gundersen, 2013; Zhang et al., 2018).

Using this framework, we hypothesize that EcM systems exert a selective pressure for a less functionally redundant soil community and attempt to maintain low pH and high C/N conditions to tightly control N cycling and maintain the dominance of their hosts (Cheeke et al., 2017; Tedersoo and Bahram, 2019; Tedersoo, Bahram, and Zobel, 2020). That is, EcM fungi dominate the soil environment enhanced by functional variation between EcM types (Chen, Koide, and Eissenstat, 2018; Zak et al., 2019), while saprotrophs and pathogens may be supressed and less functionally diverse. In addition, N-transforming microbes as well as predators and grazers may also be functionally less diverse (Fig. 2) (Averill and Hawkes, 2016; Chen et al., 2019; De Wandeler et al., 2018; Moore et al., 2015). Thus, EcM systems may experience less temporal soil community turnover, have reduced functional redundancy within the soil community, and place a direct selective pressure on beneficial organisms (Fig. 2) (Deveau et al., 2016; Frey−Klett et al., 2005), representing a more tight and closed nutrient acquisition strategy within the holobiont.

By contrast, AM systems with more homogenous functional variation within AM fungi (Chagnon, Bradley, Maherali, and Klironomos, 2013), nevertheless, may facilitate greater multifunctionality within the soil community in

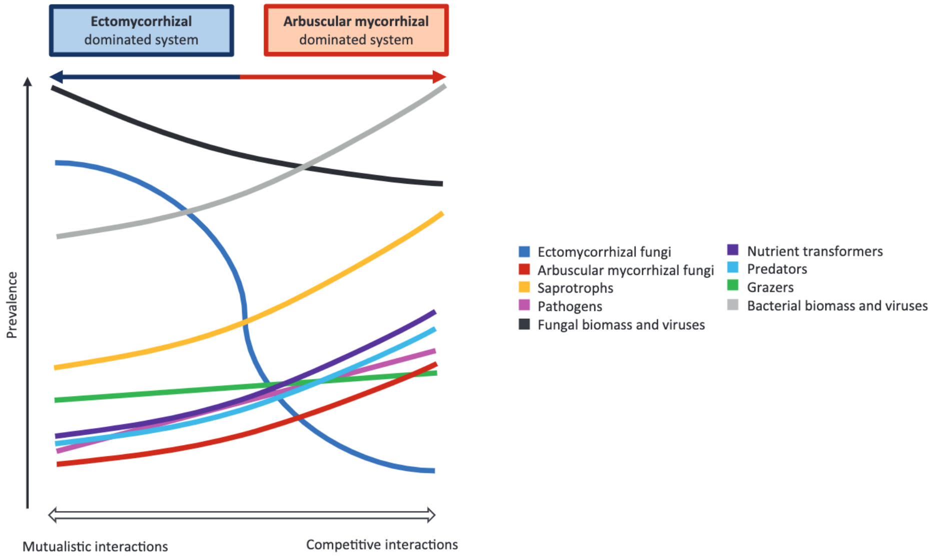

**Fig. 2.** Conceptual diagram exploring the relative prevalence of different soil organism groups as a system goes from EcM host dominance to AM host dominance, and in accordance from more mutualistic interactions to more competitive interactions. In EcM systems compared to AM systems, fungal biomass and viruses are greater than bacterial biomass and associated viruses, EcM fungi are the dominant soil guild, saprotrophs, nutrient transformers, predators, pathogens, and AM fungi are all less prevalent and potentially suppressed, while those that are present are likely to have more neutral or beneficial interactions with EcM trees and fungi, compared to more competitive and antagonistic interactions with AM trees and fungi.

## BOX 2. EcM and AM systems under environmental change

**EcM and AM systems may respond differently to environmental change, such as accelerated climate change, due to their unique C and nutrient dynamics driven by interactions between a greater ecosystem with trees, their mycorrhizal symbionts, and the entire soil community (Cheeke et al., 2017). Warming, changing precipitation patterns, and alterations to N availability stand to benefit AM systems more than EcM systems, due to a more flexible nutrient acquisition strategy and a lower C cost for the host (Soudzilovskaia et al., 2015; Jo et al., 2019; Pugnaire et al., 2019; Steidinger et al., 2019), and as we propose here due to greater functional redundancy. Dual EcM-AM trees may also become increasingly more common due to their ability to colonize new areas and function under a wider variety of fluctuating environmental conditions (Gerz et al., 2018; Teste et al., 2019; Moyano et al., 2020). Recent research has shown EcM systems to experience greater negative alterations to their functioning compared to AM systems under environmental change, including enhanced decomposition of SOM (Kumar et al., 2020), decreased EcM tree performance (Fernandez et al., 2017; Wheeler et al., 2017; Averill et al., 2018; Jo et al., 2019; DeForest and Snell, 2020), and decreased prevalence and colonization by EcM fungi (Kilpeläinen et al., 2017; Boeraeve et al., 2019). Within EcM fungi as a guild there may be a shift in dominance to short contact types that are less C-demanding and form less extensive external mycelia, and thereby reducing the overall presence of EcM fungi in the soil (Fernandez et al., 2017; León−Sánchez et al., 2018), hinting at reduced functional redundancy. These results point towards AM systems potentially benefiting more from environmental change in many cases compared to EcM systems which may be inhibited, in line with their opposing open and closed nutrient acquisition strategies, differing C costs for their hosts, and proposed contrasting functional properties of their soil communities.**

general (Fig. 2) (Battini, Cristani, Giovannetti, and Agnolucci, 2016; Rillig, 2004). The associated soil communities will experience a greater range of pH and C/N conditions, and a looser N cycle (Averill et al., 2019; Phillips et al., 2013), and may also be more functionally redundant (Banerjee et al., 2016), with less capacity for organisms to reach monodominance both below and above ground (Rillig, 2004; Tedersoo, Bahram, and Zobel, 2020; Yang, Wagg, Veresoglou, Hempel, and Rillig, 2018). They are thus representing an open and loose nutrient acquisition strategy and a holobiont strategy, which involves highly precise nutrient foraging by AM fungi to supplement more passive plant nutrient uptake in a highly competitive soil environment rather than an overall control on nutrient cycling (Chen et al., 2018; Phillips et al., 2013). This has obvious implications for C and nutrient dynamics under global environmental change.

## Future directions

We have put forward that AM and EcM systems may vary greatly in their effects on soil communities and ecosystem functioning. Hence there is a strong need to study AM and EcM systems across biomes, tree types, and edaphic gradients in order to get a more complete picture of these systems and their functioning. Specifically, further research is needed to untangle mycorrhizal type effects from environmental filtering, and whether in fact different mycorrhizal systems have the capacity to reinforce environmental controls on nutrient dynamics by actively manipulating the biotic and abiotic environment in their zone of influence. One approach to do so is to study these contrasting mycorrhizal types together in controlled environmental settings such as mesocosms, greenhouse experiments, or at least under the same edaphic conditions such as in common garden experiments. In addition, there continues to be a need for field-based studies, especially in mixed or neighboring EcM and AM systems in underrepresented regions such as tropical forests, temperate forests of the southern hemisphere, tree line ecotones, and boreal forests where some sparse occurrences of AM-forming trees occur. We further call upon researchers studying any processes and organism groups (both above and belowground) in forests to consider the presence and relative dominance of AM and EcM trees to help further understand these systems. The ease of this is facilitated by a recent plant mycorrhizal status database (Soudzilovskaia et al., 2020). We also recommend researchers studying soil processes in EcM and AM systems to study multiple soil organism groups simultaneously, something that will be facilitated by constantly improving molecular methods and cross-disciplinary collaborations (Baldrian, 2019). In line with assigning trees with a mycorrhizal status, there is also a need to continue to consider the presence of mycorrhizal associations by assessing colonization and biomass measurements or proxies of these (Soudzilovskaia et al., 2015), as well as considering the contribution of and further exploring the ecology of different functional types within mycorrhizal guilds. Finally, there continues to be the need to incorporate EcM and AM system dynamics into models predicting terrestrial processes and environmental change.

## Declaration of Competing Interest

None.

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Plant-fungal symbioses are essential to the functioning of plant-soil systems, but little is understood about how they affect the broader microbial communities they interact with. Mycorrhizal and dark septate endophyte associations were found to influence soil, root, and leaf microbiomes at the vegetation community level regionally and at the tree species level across Europe. These findings suggest that plant-root symbiont interactions are a key factor driving the structure and function of microbiomes in plant-soil systems and the processes they facilitate.

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